

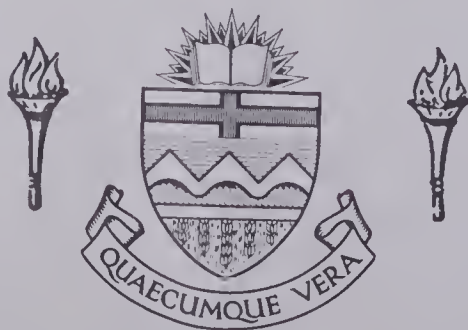
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Biological Studies of Arctic Bumblebees

by



Kenneth William Richards

A thesis

submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements for the
Degree of Master of Science

Department of Entomology

Edmonton, Alberta

Date ...*Spring*...*1970*.....

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University of Alberta
Faculty of Graduate Studies

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled: Biological Studies of Arctic Bumblebees submitted by Kenneth William Richards in partial fulfillment of the requirements for the degree of Master of Science.

Abstract

Morphological and physiological adaptations for survival of Bombus (Alpinobombus) polaris and Bombus (Alpinobombus) hyperboreus at Lake Hazen, Ellesmere Island, N.W.T. are considered. Individuals of B. polaris established natural nests in habitats where they were able to make maximum use of the energy of direct solar radiation. The queen **laid** all first brood eggs in a single cell at one time and she fed her male and female brood mixtures of pollen and honey. Behavioral shifts in flight activity in response to the continuous light occurred such that the queen flew throughout a 24 hour cycle while the workers did not. Morphological and physiological characteristics such as long shaggy hair and large body size allow the bumblebees to fly during low temperatures. The bees use flowers of a wide range of species for nutrition. Nest temperatures are similar to those of other species of Bombus. B. polaris and B. hyperboreus are in a host-parasite relationship respectively.

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My thanks are to Dr. W. G. Evans, chairman of my committee, for help and guidance during this study. Appreciation is extended to G. E. Ball, Entomology Department, University of Alberta, for discussion during the progress of writing the thesis.

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Autobiographical Sketch

My early interest in entomology was stimulated by Dr. Ruby Larson when I joined her Junior Science Club of Lethbridge. Under her encouragement and guidance I entered and won various categories of the insect collecting competition sponsored by the Entomological Society of Alberta. During high school my interest in bumblebees was stimulated by association with G. A. Hobbs, Research Station, Canada Department of Agriculture, Lethbridge and by competing in the Lethbridge and District Science Fair. During my last year of high school I was adjudicated the Grand Award at the Lethbridge Science Fair and given the privilege to represent Lethbridge at the Canada Wide Fair in Montreal. There I was adjudicated a third in the biological section with a project on "Bees and Pollination." I obtained my B.Sc. in general biological sciences in 1967 from the Lethbridge Junior College and the University of Alberta, Edmonton. A summer (1966) was spent with P. Pankiw (CDA, Beaverlodge, Alberta) as a research assistant in honey bee management. When applying for admittance to graduate school I proposed a study on alpine bumblebee biology in Southern Alberta; Dr. Hocking suggested the study of arctic bumblebees at Lake Hazen, N.W.T. As this was an opportunity to study a group of not well known bumblebees, to explore and to travel a new land, I accepted.

Table of Contents

	Page
Introduction.....	11
Systematics and Zoogeography.....	13
Habitat.....	22
Artificial Domiciles.....	22
Introduction.....	22
Materials and methods.....	22
Results.....	25
Discussion.....	25
Natural Nests.....	27
Introduction.....	27
Materials and methods.....	28
The search for nest sites.....	29
Areas in which the queen establishes natural nests.....	34
Nest construction.....	40
Discussion.....	43
Colony Development.....	45
Colony Composition.....	45
Introduction.....	45
Materials and methods.....	46
First brood.....	48
Second and third broods (sexuals).....	51
Honey pots.....	57
Population structure.....	57
Discussion.....	60

	5
Flight Activity.....	70
Introduction.....	70
Materials and methods.....	71
Frequency of food collecting at the nest entrance.....	72
Flight in the foraging area.....	90
Discussion.....	91
Nest Temperature.....	97
Introduction.....	97
Materials and methods.....	98
Results.....	98
Discussion.....	101
Food Preference.....	104
Introduction.....	104
Materials and methods.....	106
Flower preferences.....	107
Discussion.....	114
The Association between members of <u>Bombus hyperboreus</u> and <u>Bombus polaris</u>	116
Introduction.....	116
Observations.....	118
Discussion.....	121
General Discussion and Conclusions.....	124
References.....	130
Appendix.....	150

List of Tables

	Page
Table 1. Temperatures taken at various hours of the day in abandoned lemming holes investigated by <u>B. polaris</u> queens, June 3 to June 23, 1967 and June 15 to July 3, 1968, at Lake Hazen, N.W.T.	31
Table 2. Soil temperatures of a marsh and sedge meadow (M7, Fig. 5) on three different days in 1968 at Lake Hazen, N.W.T.	33
Table 3. The principal bryophytes from 92 <u>B. polaris</u> natural nests from Lake Hazen, 1967, 1968.....	41
Table 4. Numbers of first, second, and third broods of eggs, larvae, and pupae from nests of <u>Bombus polaris</u> at Lake Hazen, N.W.T., 1967 and 1968.	58
Table 5. The numbers of eggs laid per egg cell of male and female broods per year.	59
Table 6. Duration of development in days of egg, larvae, and pupae of first, second, and third brood of <u>Bombus polaris</u> at Lake Hazen, 1967 and 1968.	61
Table 7. Comparison between the brood composition and development of <u>B. balteatus</u> and <u>B. polaris</u>	62
Table 8. Maximum and minimum diel periodicities of weather factors near the ground at Lake Hazen, N.W.T.	74
Table 9. Duration of flight activity of castes and sexes of <u>B. polaris</u> and <u>B. hyperboreus</u> at Lake Hazen, N.W.T., 1967 and 1968.	91

Table 10. Number of observations of <u>Bombus polaris</u> and <u>Bombus</u> <u>hyperboreus</u> at flowers of various species at Lake Hazen, N.W.T., 1967 and 1968.	108
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List of Figures

	Page
Fig. 1. Distribution map of <u>Bombus</u> (<u>Alpinobombus</u>) <u>polaris</u>	15
Fig. 2. Distribution map of <u>Bombus</u> (<u>Alpinobombus</u>) <u>hyperboreus</u>	16
Fig. 3. Two basic types of small, light weight artificial domiciles..	24
Fig. 4. Numbers of <u>B. polaris</u> queens observed investigating different lemming hole tunnel directions at Lake Hazen, N.W.T., 1967 and 1968.....	35
Fig. 5. Distribution map of <u>B. polaris</u> natural nests in the Lake Hazen study area.....	37
Fig. 6. Generalized hummock or moss mound. a. Number of nests of <u>B. polaris</u> per quarter hummock or moss mound. b. Number of nest entrances facing different directions.....	39
Fig. 7. Typical marsh and sedge meadow (K8) in which <u>B. polaris</u> queens established natural nests. Stakes indicate location of nests.....	49
Fig. 8. First brood cell of <u>B. polaris</u> with honey pot and brood with wax-pollen canopy intact.....	49
Fig. 9. Exposed first brood larvae showing them in a curled position.....	52
Fig. 10. Second brood (male) eggs on top of first brood cocoons; the eggs have been exposed to show their horizontal position. The position of the thermistor-thermometer probe for measuring brood temperature is shown.....	52

- Fig. 11. Second brood egg cells on the outside tops of the cocoons that formed the sides of the incubation grooves..... 53
- Fig. 12. Same brood cell as above with the two groups of eggs exposed showing the front half of the incubation groove covered first..... 53
- Fig. 13. Close-up of pollen receptacle on the side and beneath the second brood (male) larvae..... 54
- Fig. 14. Egg cells of the third brood (queens) on top of the newly spun male cocoons. The large pollen receptacle is beside and beneath the male cocoons..... 54
- Fig. 15. Brood exposed showing male cocoons (centre top and bottom), exposed last-instar queen larvae (right), egg cells on top of male cocoons, and pollen receptacle (extreme right)..... 56
- Fig. 16. One queen egg cell (left) to emerge and many honey pots (top centre) nearly empty..... 56
- Fig. 17. Flight activity and nest temperature June 23-June 24, one queen, 17 first brood larvae..... 80
- Fig. 18. Flight activity and nest temperature June 30-July 1, one queen, 17 first brood pupae, 10 second brood eggs..... 81
- Fig. 19. Flight activity and nest temperature July 6, one queen, 16 workers; second brood of 14 last-instar larvae, 10 early pupae; 10 third brood eggs..... 82
- Fig. 20. Flight activity and nest temperature July 12, one queen, 14 workers; second brood of 24 late-pupae; third brood 6 eggs, 10 mid-larval..... 83

- Fig. 21. Flight activity and nest temperature July 18, one queen, 10 workers, 3 males; second brood 21 pupae; third brood 6 eggs, 10 pupae..... 84
- Fig. 22. Flight activity and nest temperature July 24, 9 workers, 5 fall queens, 2 males; third brood 5 pupae..... 85
- Fig. 23. Flight activity and nest temperature July 9, one queen, 14 workers..... 86
- Fig. 24. Flight activity and nest temperature July 11, one queen, 14 workers..... 87
- Fig. 25. Flight activity and nest temperature July 14, 15, 19, one queen, 8 workers..... 88
- Fig. 26. Flight activity and nest temperature July 21, one queen, 8 workers..... 89
- Fig. 27. Profile of air temperature on 1. June 30, 2. July 5, 3. July 15, and 4. July 31. X marks the estimated height of flying of queens and workers on those days..... 92
- Fig. 28. Period of utilization for 1967 and 1968 of the major bumblebee flowers at Lake Hazen. (Vertical line and symbols indicate first appearance.).....110
- Fig. 29. The concentration of total sugars from thin and thick honey from one nest throughout a summer. Vertical lines indicate 1 SD each side of mean.....113.

Introduction

Bumblebees have been known since the days of the first explorers, to occur in the Arctic Nearctic Region, but no extensive biological investigations of these bumblebees have been undertaken, and thus, many questions about their survival have remained unanswered. The purposes of this study are to establish the types of adaptations arctic bumblebees have for survival under arctic conditions. These purposes include studies on the type of bumblebee they are; where and how they live; feed; regulate their daily and seasonal activity, and reproduce; and what evolutionary and selective pressures are operating on them.

Investigations were conducted at Lake Hazen ($81^{\circ} 49' \text{ N}$, $71^{\circ} 18' \text{ W}$), Ellesmere Island, Northwest Territories, Canada, in the study area described by Savile (1964). The investigations were made during the periods May 24 to August 20, 1967, and May 30 to August 28, 1968. Two species of Apidae, Bombus (Alpinobombus) polaris Curtis, 1835, and Bombus (Alpinobombus) hyperboreus Schönherr, 1809, were encountered in the study area. The majority of the observations involved B. polaris because it was more abundantly represented.

Linear measurements are in the metric system, temperatures on the Celsius scale, time is Eastern Standard Time. Flower nomenclature follows that of Porsild (1964) and Savile (1964) and bryophyte nomenclature is that of Brassard (pers. comm., 1969).

References to important previous work are given in the appropriate sections, but mention should be made here of the more general papers of Hobbs (1964-1968), whose studies on comparative brood-rearing behavior

include seven of nine Nearctic subgenera, and Hasselrot (1960) who provided a basis for many aspects of this work.

Systematics and Zoogeography

The high degree of polymorphism exhibited by the species of the subgenus Alpinobombus Skorikov, 1914 and the lack of communication between North American and European workers in describing new species from early arctic explorations has resulted in a lengthy synonymy. An explanation is required of the genus- and species-group names inclusive. The subgeneric limits as erected by Franklin (1913) (= kirbyellus group), Frison (1927a), and Richards (1931, 1968) are followed. Skorikov (1922) treated Alpinobombus as a genus instead of a subgenus, and Milliron (1961) included this subgenus in synonymy of Megabombus (Megabombus). Richards (1968) gives reasons for rejecting Milliron's revised classification.

To Alpinobombus belong the following species: alpinus Linné, hyperboreus Schönherr, polaris Curtis, balteatus Dahlbom, (= kirbyellus Curtis), neoboreus Sladen, kincaidii Cockerell, and strenuus Cresson. Skorikov (1937) and Richards (1931) described the color variation within each species and Richards (1931) outlined the synonymy, most of which I accept. However, one aspect of the synonymy is not correct. The name Bombus arcticus Kirby, 1824 used by Richards (1931) is a secondary junior homonym of Apis arctica Quensel, 1802. (The latter name is a junior subjective synonym of Bombus agrorum Fabricius, 1793). Thus Kirby's arcticus must be replaced by another name. The name Bombus polaris Curtis, 1835, a junior subjective synonym of B. arcticus Kirby, is available, and is used here as the valid name of the relevant taxon. Richards (pers. comm., 1969) accepts this name change.

A thorough revision of the subgenus Alpinobombus with new taxonomic characters is required. This new system must take account of the geographical variation in melanism and structural characteristics. However it will be difficult as most of the species are represented in collections by few individuals and many arctic and alpine localities have not been investigated.

Members of Alpinobombus are confined to arctic and alpine tundra in the Holarctic Region. They are found in the Alps, Arctic Europe, Asia, Greenland, Arctic America, and in the mountains of western North America as far south as Arizona. Bombus polaris (Fig. 11) and B. hyperboreus (Fig. 2) are probably circumpolar forms. The small gaps in species ranges in Siberia are probably the result of lack of collecting. Until recently the lack of records from Arctic Canada, Alaska, Yenissei and Lena River regions of Siberian Russia made it seem that these species were "amphiatlantic" or "Eur-American" in distribution. These terms mean that the species are common to Europe and North America but absent from Asia (Lindroth, 1957). Thus the distribution of these species seemed to be examples of direct faunal exchange across the North Atlantic. Obviously, the distribution patterns are not those of "amphiatlantic" species.

In explaining the distribution of the present day forms, one must remember that bumblebees are strong fliers and may have crossed the North Atlantic to Greenland and North America. However, it is easier to assume these two species emigrated to North America across the Bering land-bridge during Tertiary and Pleistocene time as this is considered by Lindroth (1957) as the most important link towards the evolution of



FIG. 1 DISTRIBUTION MAP OF BOMBUS (ALPINOBOMBUS) POLARIS



FIG. 2 DISTRIBUTION MAP OF BOMBUS (ALPINOBOMBUS) HYPERBOREUS

the circumpolar fauna. Once the species were in North America their ranges probably advanced and receded with the last glaciation (Würm, Wisconsin) which covered the arctic islands and mainland, or the species may have survived in glacial tundra refugia (Rand, 1948, 1954, Macpherson, 1965, Leech, 1966, Hoffman and Taber, 1967). They probably emigrated from Ellesmere Island across the Kennedy and Robeson Channels to Greenland. Lindroth (1957) indicated that within the arctic of the entire northern circumpolar area the comparatively narrow strait between Baffin Island and Greenland has constituted a most effective barrier to the dispersal of animals.

McAlpine (1964, 1965a) indicated that members of only a small number of species live in the Northwest Queen Elizabeth Islands because of the severe environmental influence, and these insects are extremely tolerant of harsh arctic conditions. The harshness of the environment probably excludes members of Bombus from some areas and produces some of these distribution gaps.

Generally the distribution of B. polaris and B. hyperboreus is similar; however, B. polaris is recorded from areas where B. hyperboreus is not (i.e., Quebec and Labrador), whereas B. hyperboreus is not recorded from any area except where some other member (B. balteatus or B. alpinus) of the subgenus is also recorded. Chernov (1966) and Brinck and Wingstrand (1949, 1951) illustrate this point.

The distribution of B. polaris and B. hyperboreus was determined from the literature, the specimens in the Canadian National Collection and my collection. Published records are given by Strand (1905), Sladen (1919), Friese (1923b), Richards (1931), Hellén (1933), Braendegarrrd,

Henriksen, and Spärck (1935), Skorikov (1937), Henriksen (1937, 1939), Carpenter and Holm (1939), Brinck and Wingstrand (1949, 1951), Yarrow (1955), Savile (1959), Bruggeman (1958), Ander (1965), Chernov (1966), Swales (1966), and Mosquin and Martin (1967).

The localities in which specimens of B. polaris (Fig. 1) were collected are the following:

Greenland: Cape Schmelke $81^{\circ} 50'$, Polaris Bay $81^{\circ} 30'$, Herbert Island $77^{\circ} 20'$, MacCormick Bay $77^{\circ} 40'$, Upernivik $72^{\circ} 47'$, Hareo $70^{\circ} 25'$, Karajak $70^{\circ} 25'$, Ritenbenk $69^{\circ} 44'$, Godhaven $69^{\circ} 15'$, Manermuit $68^{\circ} 36'$, Aulatsivik $68^{\circ} 10'$, Holstenborg $60^{\circ} 56'$, Søndre Isortok $65^{\circ} 35'$, Kugssuak $64^{\circ} 50'$, Godthaab $64^{\circ} 11'$, Kuaek-kuanefjord 62° , Ivigtut $61^{\circ} 12'$, Igaliko $60^{\circ} 59'$, Julianehaab $60^{\circ} 43'$, Karortok $60^{\circ} 45'$, Pamiagdhluk $59^{\circ} 55'$, Angmagssalik $65^{\circ} 31'$, Kongerdlugsuak $68^{\circ} 32'$, Sokogens Bay $68^{\circ} 42'$, Cape Dalton $69^{\circ} 24'$, Barclay Bay $69^{\circ} 10'$, Scoresby Sound $70^{\circ} 20'$, Hekla Haven $70^{\circ} 27'$, Jameson Land $70^{\circ} 25'$, Liverpool Land $71^{\circ} 00'$, Arctic Harbour 72° , Forsblad Fjord $72^{\circ} 17'$, Cape Petersen $72^{\circ} 17'$, Ellaø $72^{\circ} 50'$, Husbukta Vegasund 73° , Myggbukta, Mackensie Bay $73^{\circ} 40'$, Moskusokse Fjord $73^{\circ} 45'$, Loch Fyne $73^{\circ} 40'$, Claverings $74^{\circ} 15'$, Herschellus, Rypefjeld, Cape Mary $74^{\circ} 15'$, Cape Wynn $74^{\circ} 40'$, Danmarkshaven $76^{\circ} 46'$, Hvalrosodden, Skirbshaven, Maroussia, Port Foulke $78^{\circ} 17'$, Vildt Land $81^{\circ} 30'$.

Northwest Territories: (mainland) Hanbury Lake Portage, Groove Falls, Bernard Harbour, Spence Bay, Coppermine, Repulse Bay, Chesterfield, Baker Lake, Geillini Lake, Eskimo Lake, Padlei, Bathurst Inlet, Aklavik, Fulleton, Muskox Lake, Eskimo Point, and Quoich River. Ellesmere Island: Alert, Lake Hazen, Tanquary Fjord, Eureka, Cape Rutherford,

Rice Strait, Harbour Fjord, Goose Fjord, Discovery Harbour, Wood Creek and Jones Sound. Taylor Island. Melville Island: Cape Ross, Winter Harbour, Bailey Point, Richards Island: Kidliut Bay. Prince Patrick Island: Mould Bay. Southhampton Island: Coral Harbour. King Williams Island. Nottingham Island. Baffin Island: Frobisher Bay, Clyde Inlet, and head of inlet, Nettling Lake, Cape Dorset, Lake Harbour. Somerset Island: Hasard Inlet. Victoria Island: Holman, Cambridge Bay, Young Point.

Yukon: Herschel Island, Rampart House, Firth River, Reindeer Depot, Snag.

Labrador: Rama, Nain, Hopedale, Natak, Cutthroat harbour on Situlalik Island, Tessiujak Bay, Nagrak Fjord, Hebron.

Manitoba: Churchill.

Quebec: Ft. Chimo, Ungava Bay, Wakeham Bay, Payne Bay, Port Harrison, Great Whale River, Knob Lake, Sugluk, Cape Chedley, Burtell Bay 58 26', Port Burwell.

Alaska: Nome, Collinson Point, Kamarkok, Eagle Summit, Umiat, Atkasuk, Meade River (SW Pt. Barrow), Barter Island, Bering Sea: St. Mathew Island, Cambell, St. Lawrence Island.

Norway: Kvalsund, Dovre.

Sweden: Swedish Lappland, Uppland, Jamtland, Lappland.

Finland: Lappland.

Russia: Kola Reninsula, Novaya Zemlya (north and south islands), Yugorskiy Peninsula, Yamal Peninsula, Tiski, Waigatsch Island, Lena River estuary, Boganida River, Khatangskiy Inlet, Khatanga River.

The specimens in the CNC which have localities in Alberta and British Columbia are probably B. balteatus and not B. polaris.

The localities in which specimens of B. hyperboreus (Fig. 2) were collected are the following:

Greenland: Thule $76^{\circ} 30'$, Saunders Island $76^{\circ} 30'$, Hareo $70^{\circ} 25'$, Karajak $70^{\circ} 25'$, Atanikerdluk $70^{\circ} 02'$, Godhaven $69^{\circ} 15'$, Sydostbugten $68^{\circ} 40'$, Aulatsivik $68^{\circ} 10'$, Holstensbrok $66^{\circ} 56'$, Søndre Isortok $65^{\circ} 35'$, Kugssuak $64^{\circ} 50'$, Kvanefjord 62° , Nekamuit 62° , Ivigtut $61^{\circ} 12'$, Tassiusak $61^{\circ} 40'$, Tigassaluk $61^{\circ} 20'$, Igaliko $60^{\circ} 59'$, Julianehaab $60^{\circ} 43'$, Kongerdlugsuak $68^{\circ} 32'$, Skogens Bay $68^{\circ} 42'$, d'Aunay Bay $69^{\circ} 00'$, Cape Dalton $69^{\circ} 24'$, Barclay Bay $69^{\circ} 10'$, Scoresby Sound $70^{\circ} 20'$, Hekla Haven $70^{\circ} 27'$, Jameson Land $70^{\circ} 25'$, Florsblad Fjord $72^{\circ} 17'$, Cape Petersen $72^{\circ} 17'$, Husbukta, Vegasund 73° , Cape Humbolt, Ymerø $73^{\circ} 20'$, Hoelsbu, Moskusokse Fjord $73^{\circ} 45'$, Cape Stosch $74^{\circ} 00'$, Loch Fyne $73^{\circ} 40'$, Claveringø $74^{\circ} 15'$, Cape Mary $74^{\circ} 15'$, Danmarkshavn $76^{\circ} 46'$, (Hvalrosodden, Skibshaven, Store Sø, Vinterhaven), Port Foulke $78^{\circ} 17'$, Hochstatter Forland $75^{\circ} 10'$, Vildt Land $81^{\circ} 30'$.

Northwest Territories: (mainland) Spence Bay, Repulse Bay, Chesterfield Inlet, Baker Lake, Hanbury Lake Portage, Groove Falls, Bathurst Inlet, Bernard Harbour, Quoich River, Muskox Lake, Boothia Peninsula, Melville Peninsula, Aklavik, Richards Island, Whale Point. Ellesmere Island: Alert, Eureka, Lake Hazen, Tanquary Fjord, Goose Fjord, Haven Fjord, Harbour Fjord, Rice Straight, Jones Sound. Melville Island: Cape Ross, Winter Harbour. King Williams Island. Victoria Island: Collinson Peninsula, Wollanston Peninsula, Holmen, Cambridge Bay. Prince Patrick Island: Mould Bay. Baffin Island: Frobisher Bay, Clyde Inlet, Eclipse

Sound, Lake Harbour. Southampton Island: Coral Harbour. Somerset Island: Hasard Inlet.

Yukon: Herschel Island.

Alaska: Collinson Point, Umiat, Barter Island, Demarcation Point, Dearing, Seward Peninsula.

Sweden: Lule Lappmark. (Virihaure Ketjaure, Poulijokk, Piete, Hildomvare, Eltivare, Vuolle, Poulejaure, Vehejokk, Kappaluobal, Staloluokta), Jamtland, Torne Lappmark, Uppland.

Norway: Dovre Fjell.

Finland: Enontekio, Finnish Lappland.

Russia: Novaya Zemlya (north and south islands), Yugorskiy Peninsula, Yamal Peninsula, Anabaski inlet, Tiksi, Boganida River, Waigatsch Island, Kola Peninsula, Gavrilova, Lena River, near Moscow, Murman Coast, and SE Chukoth.

Habitat

Artificial Domiciles

Introduction

To obtain a suitable number of bumblebees to study the propagation of the natural populations, flight activity, nest temperature, food preferences and interspecific associations, attempts were made to attract queens to artificial domiciles placed in their natural habitats. Obtaining colonies in artificial domiciles is an easier management method than studying the natural nests.

Materials and Methods

Two methods are utilized by entomologists to obtain bumblebee colonies. The first is to confine naturally or artificially overwintering queens in domiciles with sufficient food, nesting material, and with constant nest temperature until the queens establish (see Sladen, 1912, Plath, 1923a, Frison, 1927a, Hasselrot, 1952, Holm, 1960, and Plowright and Jay, 1966). The second method is to place domiciles for use by overwintering queens in the habitats from which the queens are expected to emerge (see Sladen, 1912, Frison, 1926, Fye and Medler, 1954a, Medler, 1960, Hobbs, Virostek and Nummi, 1960, Hobbs, Nummi and Virostek, 1962, and Hobbs, 1967a). The techniques and results of these two methods have varied as Holm (1966) indicated.

The latter method was followed and I used small light weight domiciles of two types (Fig. 3). Each consisted of a styrofoam top, one an inverted light blue flower pot and the other a rectangular white packing box. The wall thickness of one consisted of 1/4" plywood and the other of 15 mm shellac soaked cardboard tubing with entrance holes of either 19 mm

or 25 mm diameter. A base of masonite and nesting material of upholsterers' cotton were used. A black plastic tube of one foot length of either 22 mm or 13 mm outside diameter was connected to the entrance hole. One end was cut obliquely to form a landing platform. The tunnel directions varied.

All domiciles were placed on the surface of the ground with small pebbles, soil, vascular plants and moss material placed over the tunnels. Permafrost barred the use of underground nests. A total of 200 domiciles in 10 localities in 1967 and 180 domiciles in 1968 were used. Ten domiciles of each basic type in each locality with varying combinations of hole size, and presence or absence of tunnel were used to determine preference.

The domiciles were placed in the habitats as soon as spring melt had commenced, but snow remained in some areas four to five days after placement. The habitats varied mainly in moisture and vegetation as aridity was far more important than temperature as a limiting factor in plant growth in the vicinity of Lake Hazen (Savile, 1964). The habitat classification followed that of Savile (1964). The more arid habitats were plains and slopes of sand (P10, P11, see Fig. 5), gravel (R5, Q5), clay (N8, N12), and Dryas hummocks (R9). The moist habitats were marsh and sedge meadows (F9, P6) and springy talus slopes (K3). The habitats were sampled to establish a relationship between accepted artificial domiciles and established natural nests.

As a large number of domiciles were damaged by arctic foxes, arctic hares, and musk oxen, fine-mesh chicken wire was fixed over the tops for protection of the accepted domiciles.

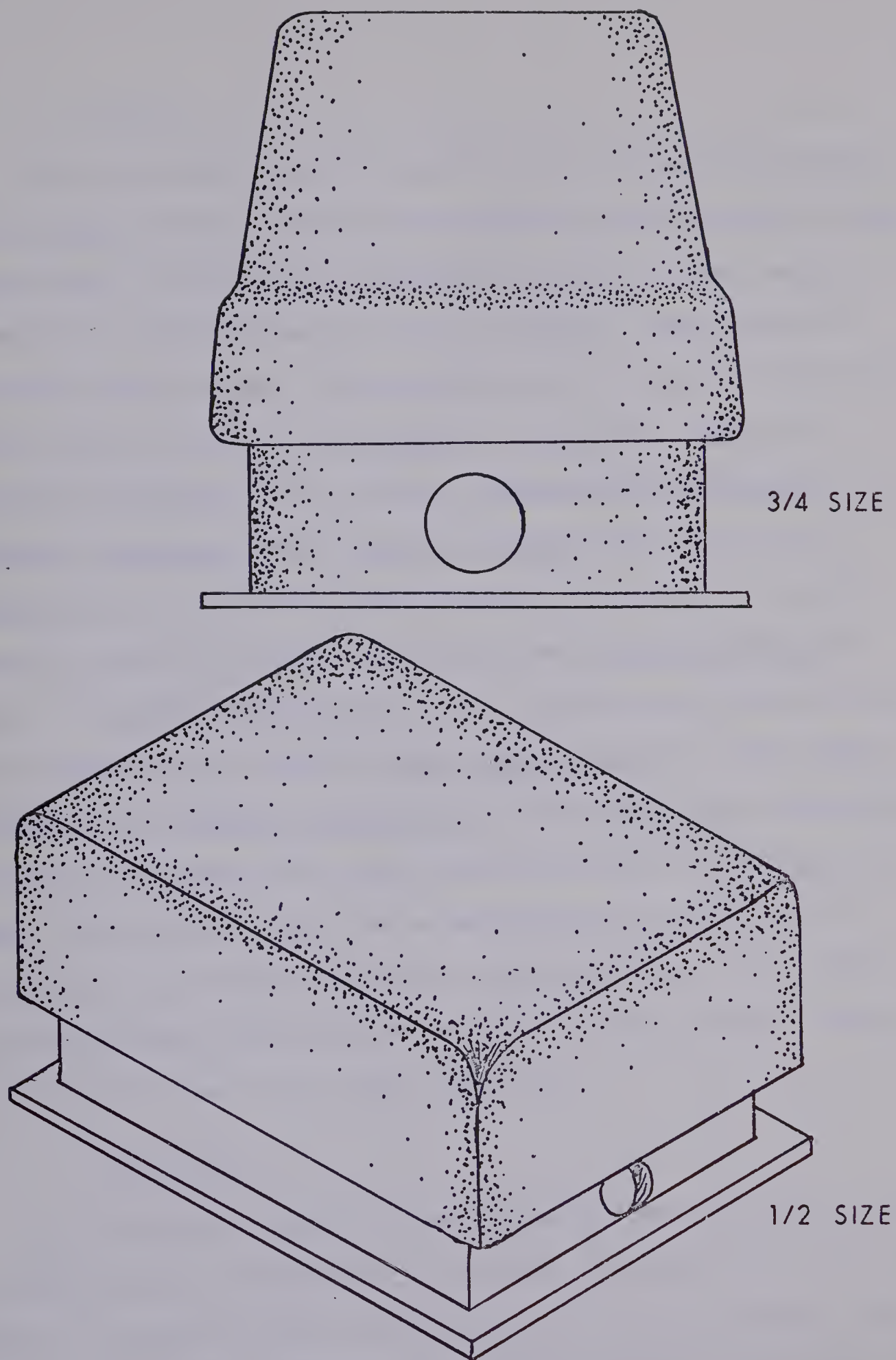


FIG. 3 TWO BASIC TYPES OF SMALL LIGHT-WEIGHT ARTIFICIAL DOMICILES

Results

During 1967, 1968 only five domiciles of one design were occupied by B. polaris queens. The light blue styrofoam flower pot with a large tunnel gave 8.7% (1967) and 2.2% (1968) acceptances. Three tunnel directions of 250°-280° range and two of 100°-115° range suggest no preferred nest entrances. Two domiciles were on a generally moist and richly vegetated habitat of Taraxacum sp., Braya spp., Draba spp., Agropyron latiglume (R. Br.) Griseb., Calamagrostis purpurascens R. Br., Erigeron compositus Pursh., Erysimum pallasii (Pursh.) Fern., and Stellaria spp. (N8, Skeleton Creek on Fig. 5). One was on a dry NW facing 45 gravel knoll (R5, Q5), with stunted Dryas integrifolia M. Vahl. and Saxifraga tricuspidata Rottb. One was on the flat clay and sand area adjacent to the camp (P11), with Oxyria digyna (L.) Hill, Salix arctica Pall., Saxifraga oppositifolia L. and Dryas in low sunk polygons. One was on a springy talus slope (K3), with a marked fluctuation in the water table and damp marsh grasses and mosses most of the year. At acceptance time, adjacent areas were completely free of snow. However, some melting snow drifts remained on N and NE facing slopes of Skeleton Creek and on slopes in the higher fault zone.

Discussion

This method of studying the natural population is actually a process in domestication of bumblebees. The use of these domiciles is not advantageous to economic entomologists as the size (area and volume) is too small for the larger colonies of the lower latitudes. On the other hand, the use of a larger styrofoam domicile may be of practical importance

to economic domestication of bumblebees because of its light weight, low cost, and structure to withstand environmental conditions. But the domiciles may be punctured and are easily destroyed by curious animals.

Failure of queens to start colonies may have resulted from the following factors:

1. the design of the domiciles
 - tunnel of too small a diameter and lacking sufficient visual contrast
 - internal volume being too large or small
 - color of domicile not attractive
2. placement of domiciles in habitats in which queens do not establish nests
3. competition from existing adequate habitats in which the queens eventually establish natural nests

The main disadvantage of the domicile method is the dependence upon the natural population to accept the domicile. Future investigators should try to gain a better insight into the factors controlling nest initiation.

Natural Nests

Introduction

When the weather becomes warmer and the spring melt commences and the first flower, Saxifraga oppositifolia is in bloom, both species of bumblebee queens emerge from their hibernation quarters after 10 months of overwintering. The first B. polaris queens were observed May 27, 1967 and June 14, 1968, the first B. hyperboreus queens on June 9, 1967, and June 21, 1968. During the first few days of the active season, the queens appeared to search for S. oppositifolia, the only flower in bloom at this time, for its nectar and pollen.

I assumed that physiological factors associated with egg development stimulate a queen to seek a nest and start a colony (Medler, 1962a). The ovaries of a B. (Bombus) lucorum L. queens in Surrey, England did not develop until after a hibernation period (Cumber, 1949a), followed by a period of active feeding. This feeding period(almost three weeks) results in a noticeable increase in weight and in swelling of the ovarioles (Cumber, 1949a, 1953). At Hazen, the pre-feeding period is one week, resulting in the ovarioles either developing rapidly in the spring or developing partially in the fall feeding period and again in the spring. Although no evidence is available, the latter is more probable because of the brief active and developmental period. I also assumed that after their ovaries mature the B. polaris queens search for nesting sites, and each eventually establishes a nest.

Several authors have reported one or two natural nests being found at any one time at lower latitudes, but few arctic and alpine natural nests have been found. In the temperate and tropical regions Gibson

(1930), Plath (1934), Cumber (1953, 1963), Michener and LaBerge (1954), Stephen (1955), and Free and Butler (1959) are some who have reported on various species of Bombus natural nests. In the arctic regions Jacobson (1898) in Friese (1904, 1908, 1923a, b), Johansen and Nielsen (1910), Frison (1919), Friese and Wagner (1912), Sladen (1919), Brinck and Wingstrand (1951), Freuchen and Salomonsen (1958), Løken (1961), and Milliron and Oliver (1966) have reported natural nests.

The purposes of this investigation are to present factors controlling nest initiation in arctic bumblebees. The areas queens rejected while searching, and the habitats in which they eventually establish natural nests were investigated.

Materials and Methods

Activity observations on bumblebees (queen, worker, or male) were noted. When a queen was nest-searching, her activity, where and what she was investigating, and possible reasons for her rejection of a particular area were described in writing. Also the temperature, moisture conditions of the soil, available nesting material, and tunnel direction were noted.

Natural nests were located by systematically searching all the major habitats. The mosses covering the nests were visible from a distance of 15 to 20 meters. Evidence for a natural nest of the year consisted of the following: in the undamaged nests, active brood development or flight activity; and in the arctic fox damaged nests, living or dead bees (queens, workers, males), pieces of brood (wax, larvae, cocoons), pollen or pollen pellets, bee faeces in nesting

material, and some type of nest material. The evidence from damaged nests varied and several possible nests were rejected because of insufficient evidence. A detailed description of the general and immediate area around each nest, as well as the nesting material assisted in establishing a habitat preference.

The days on which the queens were nest-seeking and the method of calculating the date of nest establishment follows Hobbs (1964b). This method depends upon subtracting one to six days from the date on which the establishment was discovered, depending upon the kind and amount of progress at the time. Data from the accepted artificial domiciles are included to indicate establishment peaks.

The search for nest sites

Nest hunting activity begins when the dioecious Salix arctica begins to bloom. This occurs within one week after Saxifraga oppositifolia first begins to bloom. In 1967 nest-searching lasted from June 3 to June 23 for B. polaris queens and from June 15 to July 16 for B. hyperboreus queens; and in 1968 nest-searching lasted from June 15 to July 3 for B. polaris queens and from June 23 to July 10 for B. hyperboreus queens. Nest-searching activity by B. polaris queens reached a peak four to six days after the activity began and then declined to one or two observed per day for the rest of the period. On June 19, 1968 ²⁴ B. polaris queens were observed nest-seeking whereas on June 30, only two queens were observed. The B. hyperboreus queens, even though they emerged later, also reached a peak some seven to 11 days after activity began. However, the peak was more difficult to estimate as the number

of observations at most was only three to five per day for the first two weeks and one per day after that.

Queens nest-search throughout all major habitats, but especially in cracks in the soil, in abandoned burrows of lemmings, in rocky areas, in the marsh and sedge meadows, and around the Dryas hummocks. They even searched the walls and caribou rug floors of the tents in the area. The queens fly throughout the 24 hour period if the weather is favourable, at a height of no more than 30 cm, usually less than 25 cm, alighting now and then to inspect a promising site more closely.

As the literature indicates, B. polaris and B. hyperboreus queens locate nests under the surface of the earth and in marsh and sedge meadows. Thus of particular interest were those queens which searched to establish a natural nest in the clay ~~banked~~ areas or in the abandoned holes of lemmings of the species Dicrostonyx groenlandicus Traill, or the more suitable marsh sedge meadows.

Previous biological works within the study area were by Savile (1964) who described the vegetation and moisture conditions. Day (1964), Yong (1961), and Yong, Windisch and Limperis (1962) discussed and analyzed the soil characteristics. Powell (1961) discussed the vegetation and microclimate.

Data on temperature of the abandoned lemming holes (at a depth of at least 30 cm), which the queen investigated and which were taken at different hours on different days of each year are presented in Table 1.

In comparison 75 temperature readings were recorded (at a depth in the soil of 5 cm) in a grid 25 meters long by 8 meters wide in a marsh

Table 1

Temperatures taken at various hours of the day in abandoned lemming holes investigated by B. polaris queens; June 3 to June 23, 1967, and June 15 to July 3, 1968, at Lake Hazen, N.W.T.

	Number of lemming holes investigated	Range C	Mean	SD
1967	26	-1.1--3.9	1.20	0.98
1968	39	-1.8--2.8	0.64	0.73

and sedge meadow (M7, Fig. 5). These readings were taken at 1400 on three days of complete overcast, with air temperatures at 15 cm above ground of 7.5 C, 11.0 C, and 9.5 C respectively and winds of less than 4 mph NE and are presented in Table 2. The vegetative and soil material of the marsh meadow is warmer than the air temperature in the lemming holes, and appears to be an ideal location for a queen bumblebee to establish her nest. Powell (1961) states that the mean monthly soil temperature for June (part of the nest-seeking period) at the one foot level for differing soil types near the camp in 1958 was -3.30 C, -7.83 C, and -14.52 C. Daily soil surface temperature fluctuations occur (Geiger, 1965), especially during June at Lake Hazen (Powell, 1961, Corbet, 1967b), and these fluctuations may have influenced the temperature of the marsh and sedge meadows. But the soil temperatures at the one foot level (Powell, 1961) were lower than the temperatures in the lemming holes. The latter were more exposed and influenced by the surface temperature and solar radiation. Likewise, in the lemming holes the temperatures were lower than the marsh meadow temperatures. The factors influencing the warmer marsh meadow were the surface and slope exposure, the degree of slope, hydrology, permafrost, snow cover, vegetation, grain size of soil, solar radiation and air temperature.

About 75% of the abandoned lemming holes examined contained ice or permafrost, or were extremely damp in some part of the tunnel. Perhaps this alone would deter a queen from establishing a nest. In comparison, the surface moss and liverworts of the marsh meadows were not as affected

Table 2

Soil temperatures of a marsh and sedge meadow (M7, Fig. 5) on three different days in 1968 at Lake Hazen, N.W.T. at a depth of 5 cm.

	N	Range	Mean	SD
June 17	75	0.7--7.0	4.82	1.10
June 25	75	1.5--8.5	6.35	1.28
July 2	75	3.0--12.0	8.28	1.58

by the ice and permafrost, but were briefly inundated by the fluctuating water level during snow melt. The meadows became progressively warmer during the summer season.

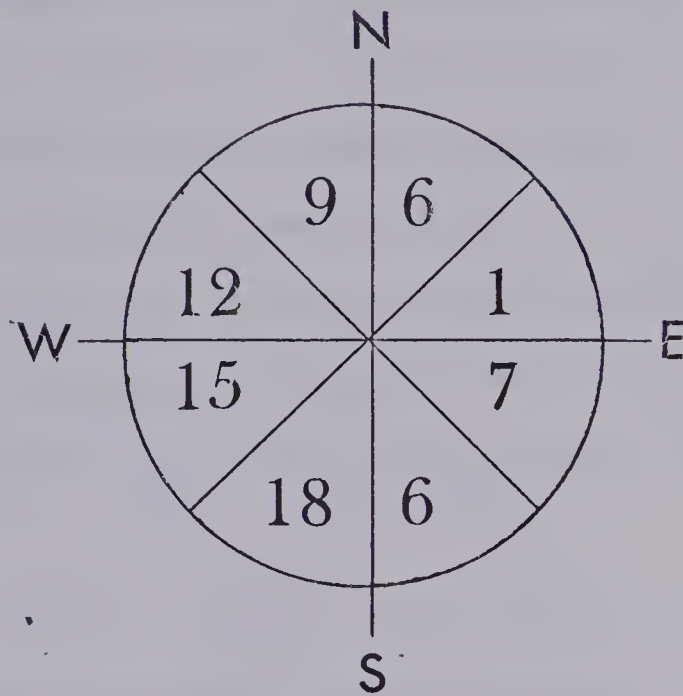
The lemming tunnel directions that the queen investigated (Fig. 4) indicate they preferred south through to northwest. The lemming tunnel diameters were in the range 4-8 cm. Usually queens investigated tunnels for less than 30 seconds, although some individuals investigated tunnels for up to three minutes. Lemming nest material of dried or decaying grasses, sedges, mosses, animal hair, and occasionally feathers were found in 27 burrows that were excavated. In comparison the marsh meadows provided more than adequate nesting material in the form of mosses, leaves, grasses and sedges. Suitable nesting material was absent from the saline clay, sand, gravel, Dryas-Kobresia areas, mud and gravel deltas, and most Dryas hummock habitats. These areas were sparsely vegetated with vascular plants and bryophytes. The marsh meadows and the dry clay banks were equally adjacent to and part of future food sources, thus lack of food would not be a deterrent for establishment at Lake Hazen.

The combined factors of low soil temperatures, excessive moisture, lack of nest material are probable reasons why the queens reject many of the habitats they investigated.

Areas in which the queen establishes natural nests

In 1967 the period of natural nest and artificial domicile establishment for nine B. polaris queens observed began on June 7 and ended June 17. The peak occurred about June 9 or June 10 when four of

Fig. 4. Numbers of B. polaris queens observed investigating different lemming hole tunnel directions at Lake Hazen, N.W.T., 1967 and 1968.



the queens established in that period. In 1968, for eight queens, the period was from June 15 to June 25 with no definite peak of establishment. Three queens, while in the process of establishing, abandoned their nests, apparently because of disturbances during examination. Four queens failed to return to their nests after a light snow storm on June 29, 1968, when the screen temperature was 1.0 C.

Ninety-four natural nests were located at Lake Hazen and one was reported by colleagues from Per Ardua glacier camp at the head of Tanquary Fjord. Ninety-two of the nests were on the surface of the ground, two on caribou rugs in the sleeping tents, and one in an abandoned lemming hole.

Nests are clumped in the study area (Fig. 5). The position of the accepted domiciles is included. This distribution is related to the drainage of the two streams in the area, namely Skeleton Creek and creek no. 51. There were a few nests (i.e., those in T6, Q7, P6, M10, of Fig. 5) that were not along these streams, but these areas possessed the characteristics of the marsh and sedge meadows as they were adjacent to pools and tarns. The three nests described by Milliron and Oliver (1966) were found in the areas designated as marsh meadows.

The general characteristics and vegetation of the marsh and sedge meadows (Fig. 7) and the marginal areas around each of the pools and tarns has been described by Savile (1964) and Oliver and Corbet (1966). Plants found in the moister meadows are Juncus albens (Lge.) Fern., J. castaneus Sm., J. biglumis L., Eutrema edwardsii R. Br., Cardamine pratensis L., Saxifraga hirsulus L., and Ranunculus trichophyllus Chaix. The principal mosses are Drepanocladus brevifolius (Lindb.) Warst. and

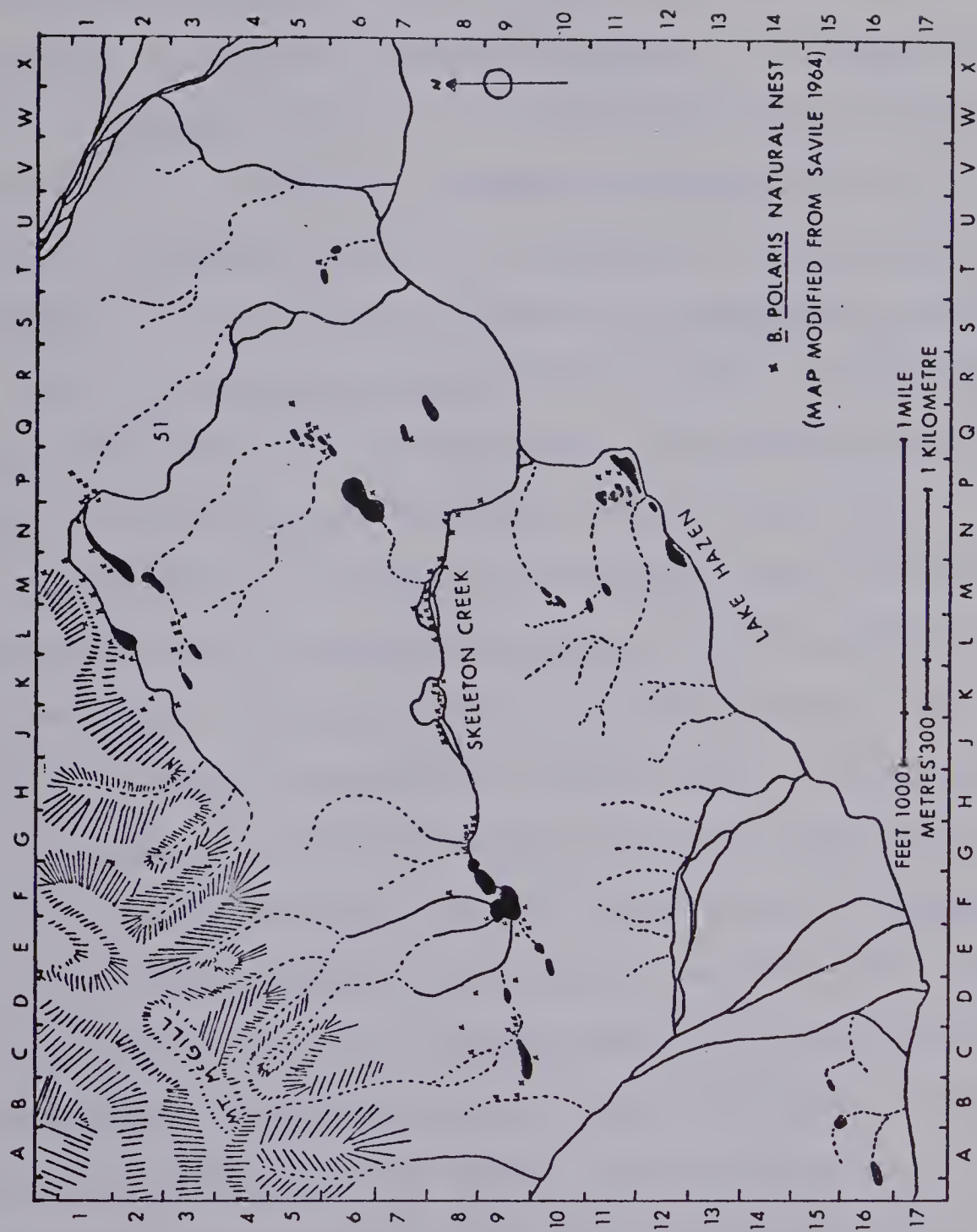
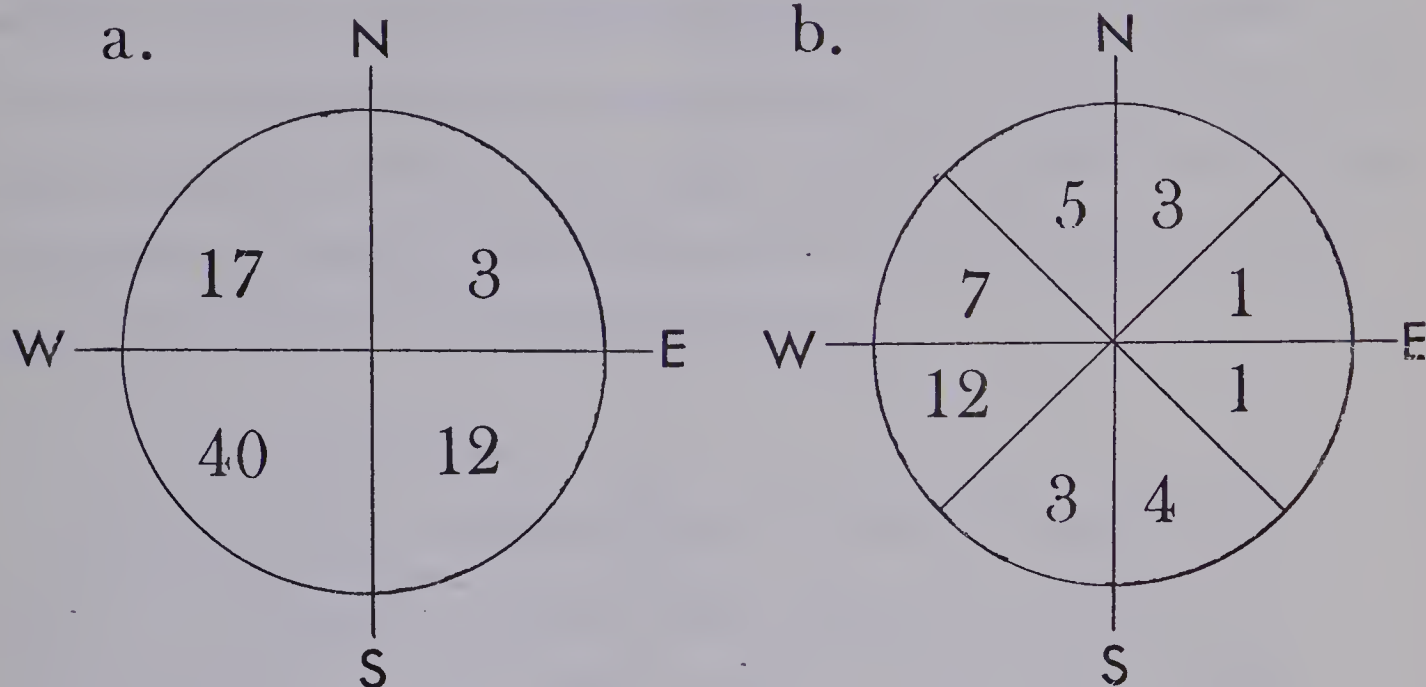


FIG. 5 DISTRIBUTION MAP OF *B. polaris* NATURAL NESTS IN THE LAKE HAZEN STUDY AREA

Bryum spp. The drier meadow areas are characterised by the dominant Carex aquatilis Wahlenb. var. stans (Drej.) Boot., with varying amounts of Eriophorum scheutzeri Hoppe, E. triste (Th. Fries.) Hadac and Love, J. biglumis, A. latifolia, Polygonum viviparum L., S. arctica and lesser amounts of Equisetum arvense L., E. variegatum Schleich., Pedicularis arctica R. Br., P. hirsuta L., Cerastium beeringianum Cham. and Schlecht., Saxifraga nivalis L., S. rivularis L., and Ranunculus sulphureus Sd. The principal bryophytes are Drepanocladus revolvens (Sw.) Warnst., Orothecium chryseum (Schultes) BSG., and Campylium arcticum (Williams) Broth., and Bryum spp. The vegetation forms a closed cover over the partly decaying organic material (Day, 1964).

In the meadows and marginal pool areas the natural nests were found on small flat areas, in depressions and beside small hummocks of moss or other vegetation. Variations in structure were numerous. If a generalized hummock or moss mound is taken to have a circular shape (Fig. 6), then the majority ($P = 0.005$) of the nests (Fig. 6a) for which direction is available are in the 180° to 270° quadrant. Similarly, more nest entrances (Fig. 6b) were found in the 225° to 270° range. A possible explanation is the combined factors of sun position and peak in temperature. The maximum diel soil surface temperature falls near 1300-1600 hours (Corbet, 1966, 1967b), which is related to a comparatively high solar altitude in the 195° - 240° position at that time. Corbet (1967b) installed probes around a conical mound of moist moss and found highest temperatures occurred at the west, not at the south where the sun's altitude was greatest and that the surface temperature of the north slope remained almost steady through the 24

Fig. 6. Generalized hummock or moss mound. a. Number of nests of B. polaris per quarter hummock or moss mound. b. Number of nest entrances facing different directions.



hours. He also found that the moss mounds and Dryas hummocks in sedge meadows are warm areas, at all time of the day and show exceptional marked diel periodicities of surface temperatures. Moderate to light moisture conditions were not deterrent factors in nest establishment as the nests often became water logged beneath, but remained comparatively dry on the surface. Nests in the sedge meadows and along the north bank of the streams were drier, but any moisture found in and around these nests resulted from the later permafrost melt.

Nest Construction

Upon accepting a suitable habitat to establish a natural nest (Fig. 7) or occupying a domicile a queen completely rearranged the nesting material, of either moss or cotton, to form a brood chamber. In loosening and rearranging the moss she pulls it with her mandibles and fore-legs and with her mid- and hind-legs pushes it under her body to the desired position. The queen and later assisting workers, continue to rearrange as long as the colony is expanding. Most nesting material consisted of mosses and liverworts. The names of the principal bryophytes from 92 nests are presented in Table 3. The principal vascular plant-nesting material consisted of dried blades of C. aquatilis and Eriophorum spp. with Equisetum spp., Dryas and Salix in some nests. A complete list of the mosses and liverworts with relative abundance from the nests is in Appendix I. In 1967, representatives of 46 mosses and four liverworts with an average of 7.1 (range 2-14) species were collected from each of the nests; in 1968, representatives of 48 mosses and liverworts with an average of 6.7 (range 3-13) species were collected.

Table 3

The principal bryophytes from 92 B. polaris natural nests from Lake Hazen, 1967, 1968

	no. of nests with moss	
	1967	1968
<u>Distichium capillaceum</u> (Hedw.) BSQ	21	19
<u>Districhum flexicoules</u> (Schwaegard.) Hampe	19	19
<u>Bryum</u> spp.	38	33
<u>Campylium arcticum</u> (Williams) Broth.	36	25
<u>Drepanocladus revolvens</u> (Sw.) Warnst.	20	28
<u>Crothecium chryzeum</u> (Schuttes) BSG.	24	29

Nest sites varied as the season progressed. At the beginning the external dimensions were small, about 5 cm diameter, whereas towards the end some were as large as 15 cm. The external covering of a nest cavity was convex-oval with the mosses and dried sedge leaves intermixed in a rather thick and tightly constructed surface. The entire covering often rose to a height of 5 cm most of which was nesting material. The nest cavities were in shallow depressions covered with dried moss, leaves, roots, and occasionally peat. The queen and workers excavated parts of the moss mounds beside the nests. The bees used these areas to defecate, thus removing any possible fungal growth on bee excretions outside the brood chamber.

The queen abandoned the brood on a caribou rug in a sleeping tent after hair had been pulled and two pollen pellets had been collected, presumably because of frequent interruptions. The other caribou rug nest also in a sleeping tent at Per Ardua glacier camp was covered with hair by the queen and developed to maturity. The one lemming hole nest (nn. 11, 1967) was found by excavation at the end of a long tunnel of 64 cm. The nest entrance was on a southwest facing light-colored clay bank (P8) on Skeleton Creek. The direction of the tunnel was about 225° with the entrance diameter of 5 cm. At the time of acceptance snow was probably present on the opposite bank. Few lemming holes were found and plants such as Salix and Dryas, were growing in the immediate area. The soil at the entrance on July 17, 1967 was 12.2 C and at excavation was damp. The tunnel turned right at 13 cm and was parallel with the ground surface at a depth of 15 cm. The nest may have been influenced by

extreme maximum soil temperatures. The brood chamber was about 10 cm in diameter and had Salix and Dryas leaves and five species of mosses in the nesting material. The nest was found under the lid of a 45-gallon barrel in the nesting material of an abandoned lemming home. A previous nest had been established as wax of larvae and cocoons and pollen was found.

Discussion

The factors controlling nest initiation are extremely complex. This study presents some of the consequential bioclimatic conditions, but ignores the physiological factors. Whatever physiological factors are involved, either hormonal or ovarian development, I assumed they must either take effect extremely rapidly after emergence from hibernation or more probably became effective during the fall feeding period and then again before or during spring emergence. The latter would be a special physiological adaptation to arctic conditions. When the queens are nest-searching for a suitable microclimatic area they search throughout all major habitats. Environmental and physiological stimuli inhibit queens from accepting many of the areas they search. However, the queens that search such areas as lemming holes give an indication that in some localities B. polaris queens establish underground. The meagre literature citations are also indicative. Another possibility is that the near ancestors of the members of Alpinobombus may primarily be underground dwellers and the trait of underground searching is a behavioral relationship to the ancestral groups.

The habitat in which the queen eventually establishes her nest is warmer than habitats of compact soil, has more suitable nesting material than the Dryas-Kobresia, sand and gravel **knolls** habitats, is equally adjacent to the food sources, and lacks the excessive moisture that the clay, sand, gravel, and Dryas hummock areas have during nest establishment. But I consider one of the most limiting factors to be temperature, as far as nest-searching and nest establishment are concerned. Low soil or lemming hole temperatures are believed to inhibit the queens from establishing in any habitat in which they have searched, even if the other factors are favourable. The diversity of nesting material indicates that the founding queens were not specific in choosing the types of material to build their brood chambers. The queens were more interested in utilizing the leaves and bracts of any moss and liverwort as nesting material. These mosses and liverworts found in the drier marsh and sedge meadows at Lake Hazen range from the rare Fissidens arcticus Bryhn., to the common D. revolvens.

Interestingly, the direction of tunnels they searched was the same, southwest, as the direction and slope where the queens established the nest. The queens exploited the incoming solar radiation by choice of habitat or by behavioral response and thus are utilizing the warmest sector of moss hummocks. Here, as in many other arctic organisms, the pattern of distribution and behavior are correlated with the aspect of the slope they inhabit (Corbet, 1967b).

Colony Development

Colony Composition

Introduction

Among the most potential aspects for adaptations in arctic and alpine bumblebees are the physiological and morphological developmental stages of a colony. Because the arctic climatic environmental factors (i.e., low temperature, small heat budget, and reduced growing season) are more severe than in other world regions the adaptive developmental changes have become important in allowing these bumblebees to survive in the high arctic. These arctic bumblebees are compared with their more temperate region relatives.

There has been little previous work on Alpinobombus brood-rearing behavior and those authors, except for two, who have investigated the various species, described only the contents of nests at the particular stage when they were collected. In the arctic, Sladen (1919) obtained full fed larvae and cocoons from an Eskimo: Frison (1919) found two nests of 35 and 20 individuals, and Frison (1927) generalized on the fecundity of arctic bumblebees and in 1922 wrote some biological notes concerning members of B. kincaidii; Brinck and Wingstrand (1951) reported a B. alpinus nest with dates of occurrence of first workers and males and a total population of some males, 12 young queens and 30 workers; Johansen and Nielsen (1910) reported a B. polaris nest with eggs, 20 empty worker cocoons, 11 mature male pupae, and 11 full grown female larvae, but no adult males or fall queens. Løken (1961) reported on the composition and population of a nest of B. polaris (= arcticus v. alpiniformis) and Milliron and Oliver (1966) reported on the

composition of three B. polaris nests from Lake Hazen. Hasselrot (1960) observed the phenology of a single balteatus (= kirbyellus) nest; and Hobbs (1964a, b) observed the brood-rearing composition of Alpinobombus. As yet, no one has studied the brood-rearing behavior of the other four species of the Alpinobombus group, although Friese (1902, 1904, 1908, 1923a, b), Friese and Wagner (1912), Sparre-Schneider (1894, 1898, 1906), Richards (1931), Downes (1962, 1964, 1965) and Swales (1966) have made general comments on the population structure and adaptations of arctic bumblebees.

For a comparison of brood development (composition, phenology, and fecundity) with more temperate and tropical forms from some of the 35 subgenera (Richards, 1968) the general works of Sladen (1912), Plath (1934), Free and Butler (1959) and Hasselrot (1960) are useful; for the species Putnam (1864), Coville (1890), Plath (1922a, 1924, 1927a), Friese (1923a), Frison (1917, 1918, 1927a, 1928, 1929, 1930a, b), Rau (1941), Richards (1946), Brian (1951a), Free (1955a, b, 1961), Taniguchi (1955), Miyamoto (1957, 1963), Wójtowski (1963a, c), Sakagami, Akahira and Zucchi (1967), Meidell (1968) are useful; and at the subgeneric level Hobbs' findings (1964a, 1965a, b, 1966a, b, 1967a, 1968) can be applied. This study relies on the more recent extensive publications of Hasselrot (1960) and Hobbs (1964-1968) for comparison of the various species and subgenera.

Materials and Methods

Observations were made and rough sketches and photographs were taken of five artificial domicile nests and of 24 natural nests at

intervals of two to five days throughout the seasons. The arrangement and number of eggs, larvae, pupae, and pollen were determined by dissecting the wax-pollen covering the broods. Nests were periodically collected and brought back to the field laboratory and the brood dissected; broods which the queens had abandoned were also brought back and dissected. The number of nests observed throughout the seasons varied because of predation, abandonment, and discovery of new natural nests.

Before experience had been gained in removing the protective covering, the workers were observed tearing out the eggs or larvae from a recently exposed wax-pollen cell and carrying them outside the nest with their mandibles. These larvae were noted and collected. I also observed workers eating the exposed eggs in egg cups which previously led Brian (1951a) to suggest cannibalism. When I exercised care and did not touch the eggs or larvae, the workers repaired the wax-pollen covering over them.

Another factor influencing brood development was the exposure of the nest during observations. In one instance, a 15 minute observation resulted in a drop in nest temperature of 8.25 C (30.25 to 22), in another, a 17 minute observation resulted in a decline of 10.0 C (31 to 21). After the queen returned and began incubating the brood the nest temperature rose to its former level. These temperature drops are comparable with those resulting from the queen's absence during foraging (Fig. 17) and, thus cannot be considered as stress factors on the brood development.

First brood

After the B. polaris queen completely rearranged the moss or upholsterers' cotton nesting material she visited flowers of Saxifraga oppositifolia or Salix arctica and returned to the nest with two pollen pellets. After placing these pellets side by side she commenced to build the wax-pollen first brood cell (Fig. 8) on top of the pellets. The honey pot was built after the brood cell in all nine cases in which the sequence was observed. The honey pot which was separate from the brood was built in line with the longitudinal axis of the incubation groove. It was sufficiently near the groove that the queen while incubating could drink from it without leaving the brood. Before the queen built the honey pot she stored honey in the moss and cotton nesting material; hence she had a small food reserve which also acted as an early insulating layer. All eggs were deposited vertically in a single cup at one oviposition. But I believe, in one instance the egg cell was reopened and additional eggs were laid as the eggs were in two separate groups within the cell. The second laying was probably a few hours after the first as all emerged about the same time. The egg cells had a definite area under them for the placement of fresh moist pollen while in larval development, thus the queen at this stage was a "pocket-maker." The wax-pollen canopy covering the egg cells was a dark brown rough mass which probably attained its color from the yellowish pollen of S. oppositifolia and S. arctica. The incubation groove, although poorly formed on the egg cell, was present in all nests observed.



Fig. 7 Typical marsh and sedge meadow (K8) in which B. polaris queens established natural nests. Stakes indicate location of nests.

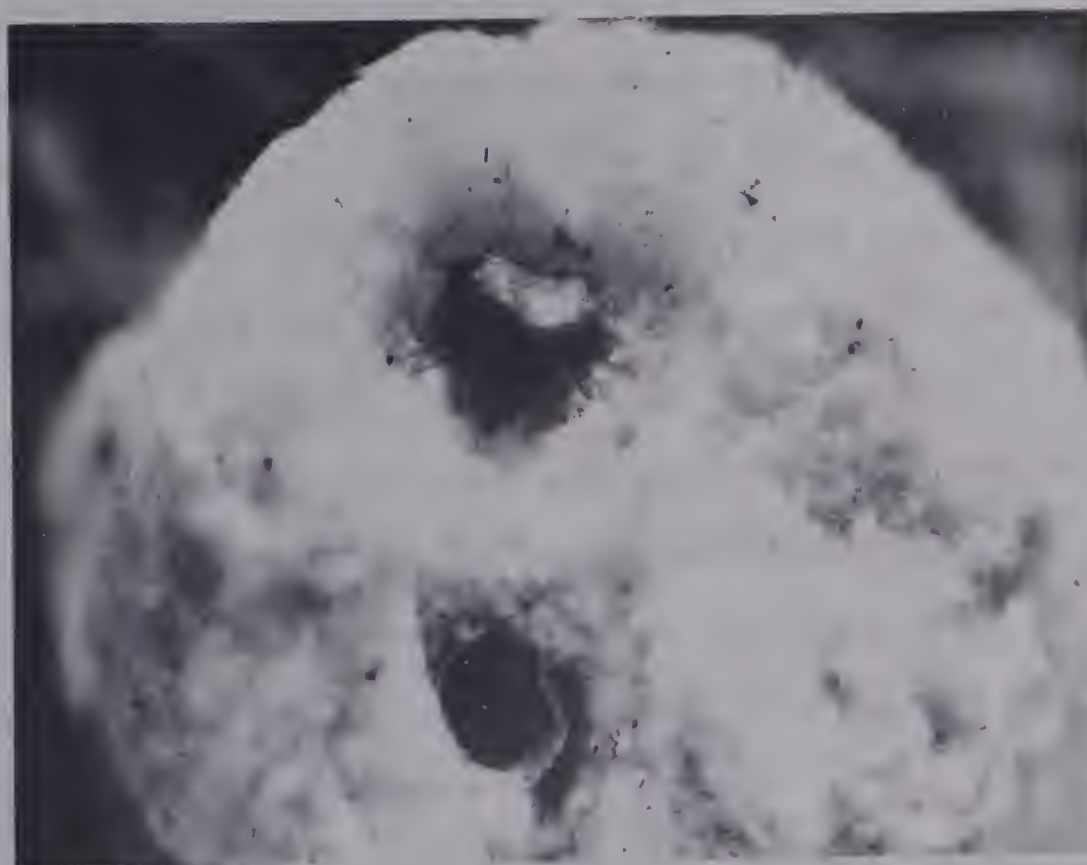


Fig. 8 First brood cell of B. polaris with honey pot and brood with wax-pollen canopy intact.

First brood larvae were fed moist, easily manipulated pollen by the queen. She pushed it under the brood in several places, especially the sides of the incubation groove. Although no measurements were taken, those larvae in the front (12 o'clock position) of the incubation groove were larger and developed more rapidly than those at the back (6 o'clock position). This is because most pollen was pushed under the brood in the former position and the honey pot was directly in front. After one to three days of growth, the larvae were side by side in a curled position (Fig. 9). This allowed easier access to the pollen below. When pollen was plentiful the larvae ate into the mass until they became completely enclosed. Last instar larvae constructed separate cells immediately before starting to spin cocoons and were then fed individually with a mixture of honey and pollen. Often they were of such a size that the wax-pollen canopy did not completely cover them. In some cases the color of the wax-pollen covering first the egg cells and then the larvae changed from a dark brown to a lighter tan. This color change was related to a change in the pollen being foraged.

The cocoons were separated from each other by flimsily spun silk and by the wax-pollen covering. No fresh pollen was brought into the nest and any pollen already present began to harden and dry. The incubation groove present from the initial egg cell was more pronounced from mid-larval stage through to worker emergence.

Members of the first brood were workers. However, in one instance three workers and 11 males (imagines and late stage pupal) were present when the nest was collected. This nest was still developing, as it had

an egg cell with 12 eggs and eight two- or three-day old larvae. The queen had abandoned the nest, apparently because no workers existed to assist her in food gathering and incubation, and the few emerged males and workers had depleted the honey in the honey pot reserve. None of the second or third brood in any nests observed were workers. The workers which emerged first were those at the 12 o'clock position (front of brood nearest honey pot) on the base of the incubation groove. Succeeding emergences progressed posteriorly through the incubation groove to the 6 o'clock position (back of brood furthest from the honey pot). Larger-sized workers emerged first, and the small workers later. There was a large size variation in workers within one nest as has been reported for other species by Sladen (1912), Cumber (1949a), and Medler (1962a, 1965).

Second and Third Broods (Sexuals)

Egg cells, also made of wax-pollen material, of the second and third broods were made on the outside tops of the cocoons that formed the sides of the incubation grooves (Fig. 10). The egg cells were made one to two days before or after the first brood larvae had begun to spin. Eggs were laid in a horizontal position (Figs. 11, 12), with the majority side by side or on top of each other. In 10 of 13 instances, the first eggs were placed in the egg cell which occupied the front half of the incubation groove. Usually, one of the ridges of an incubation groove was completely covered with egg cells before any were built on the other, but if an additional egg cell was made on the same ridge, it was not until after the first eggs had hatched. As a



Fig. 9 Exposed first brood larvae showing them in a curled position.

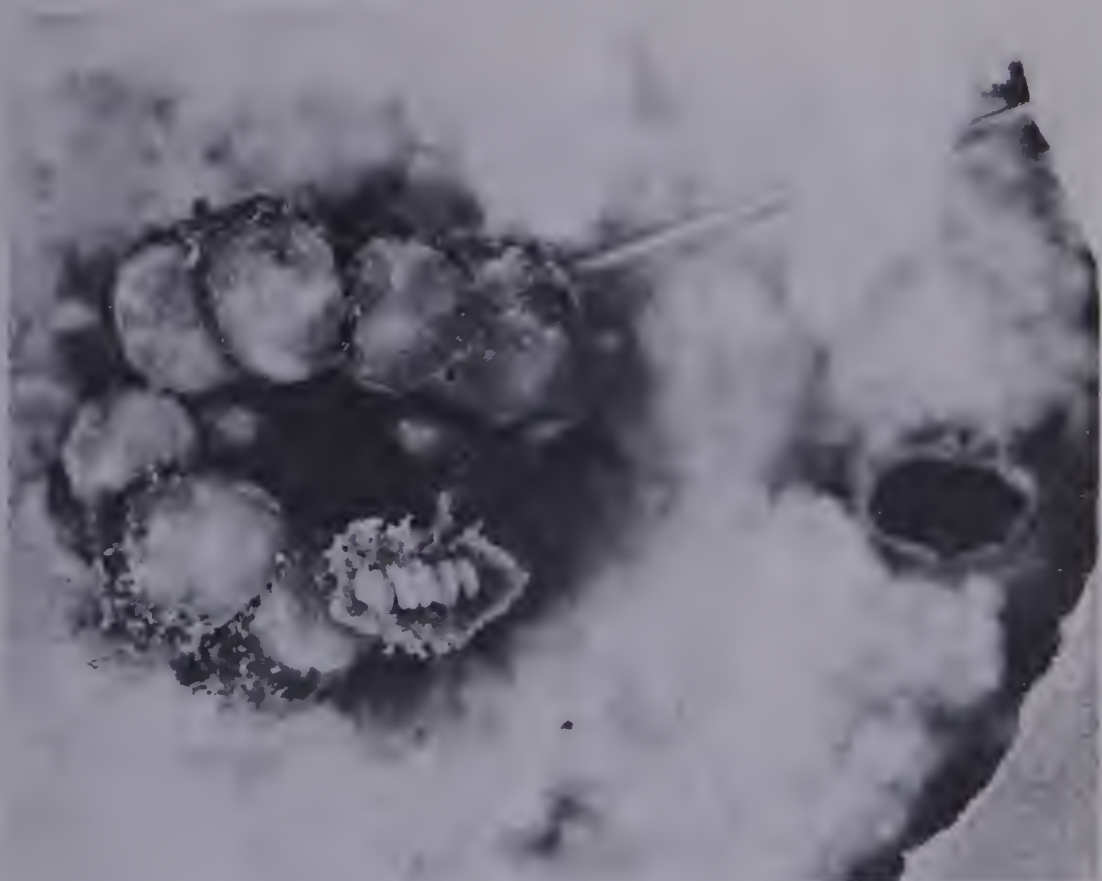


Fig. 10 Second brood (male) eggs on top of first brood cocoons; the eggs have been exposed to show their horizontal position. The position of the thermistor-thermometer probe for measuring brood temperature is shown.



Fig. 11 Second brood egg cells on the outside tops of the cocoons that formed the sides of the incubation grooves.



Fig. 12 Same brood cell as Fig. 11 with the two groups of eggs exposed showing the front half of the incubation groove covered first.



Fig. 13 Close-up of pollen receptacle on the side and beneath the second brood (male) larvae.



Fig. 14 Egg cells of the third brood (queens) on top of the newly spun male cocoons. The large pollen receptacle is beside and beneath the male cocoons.

result, brood of different stages of development could be on the same ridge. No pollen was placed in or under the egg cells to prime the eggs of the second or third broods. The egg cells were small, thick, dark brown wax-pollen cups 6-7 mm long and 3-4 mm wide, varying with the number of eggs laid in each.

When larvae on the fore part of the incubation groove hatched, the wax-pollen canopy covering was not extended to any adjacent or hind group of larvae. Therefore, the larvae beneath a canopy on any ridge were separated and were of different sizes on each side of the incubation groove. Fresh moist pollen was pushed into the pollen pocket (Fig. 13) beneath the larvae when the first eggs hatched. This pollen receptacle was built on the edges of the brood mass. The pollen pot for feeding male and queen larvae was larger than the pollen receptacles under the larvae. Thus, the bees at this stage of development became "pollen storers." The curled position and pollen diet of the second and third brood larvae were identical to first brood larvae. The last instar larvae were not always completely covered with wax as were the earlier instars, although they built separate cells. All larvae were fed pollen; larvae of sexuals were also fed honey from the honey pots. The larvae were fed by workers through holes in the wax-pollen canopies.

The cocoons were separated from each other by silk and wax-pollen coverings. Egg cells were still being built as the first male cocoons were being spun (Fig. 14). These egg cells did not develop or were removed by the workers.

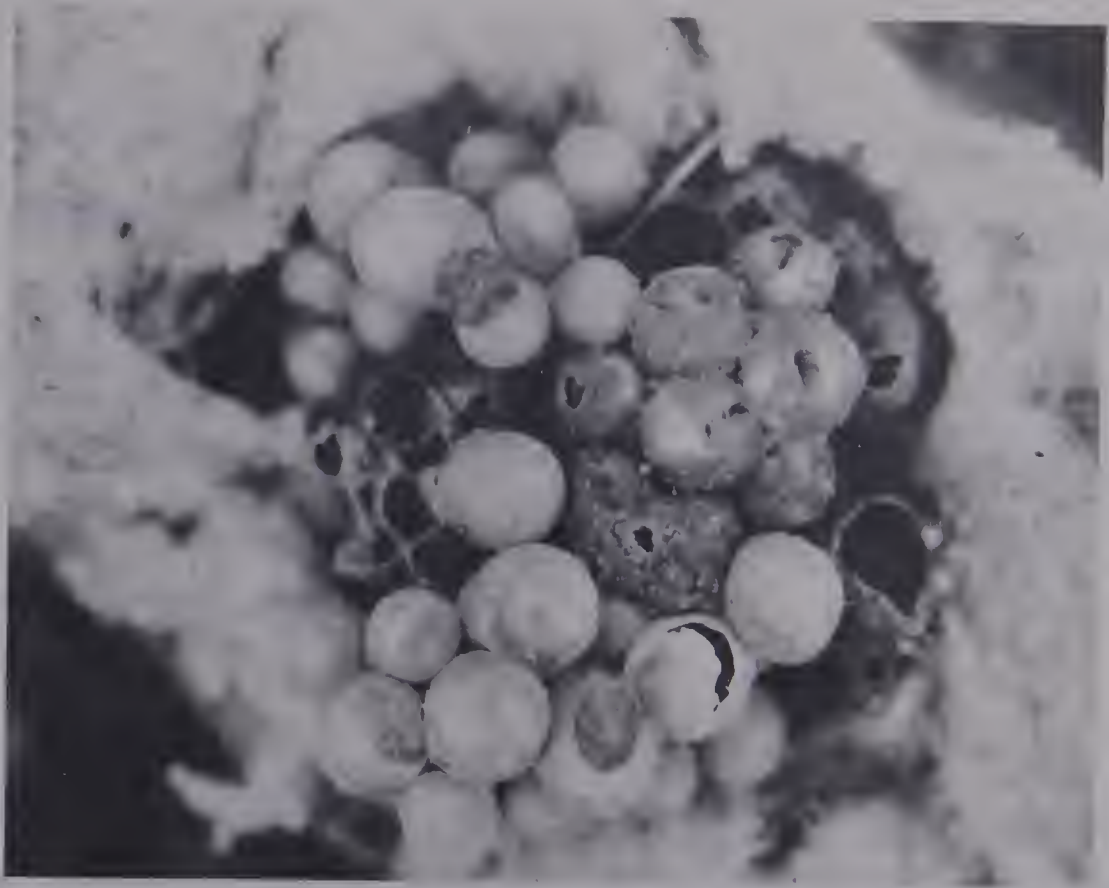


Fig. 15 Brood exposed showing male cocoons (centre top and bottom), exposed last-instar queen larvae (right), egg cells on top of male cocoons, and pollen receptacle (extreme right).



Fig. 16 All but one queen egg cell (left) emerged, and many honey pots (top centre) nearly empty.

The first egg batches of the sexual brood produced males. The remaining batches laid on the remaining part of the incubation groove or on the canopy covering the last instar larvae and early cocoons of the second brood produced queens (Fig. 15). The males remained in the nest feeding on honey up to two days whereas the queens remained up to seven. The original establishing queen remained with her nest until after the first males emerged.

Honey pots

The queen generally built two or three additional honey pots 2-3 cm high and 1-1 1/2 cm diameter across the opening before the workers emerged. These were usually 1/2 to 3/4 full. During the season the volume of each honey pot varied as first the queen and later the workers added or removed wax. While the first brood was in the egg stage two honey pots, one from each of two nests, had capacities of 1.12 cc and 1.73 cc. After the workers emerged as many as 14 honey pots were built (Fig. 16), these generally 1/2 to 3/4 full of honey. However, in times of unfavourable weather the volume decreased. Honey was also stored in some of the old worker cocoons, and the empty male cocoons, but these storage areas were at most 1/4 full.

Population structure

The population of eggs, larvae and pupae of the first, second, and third broods for each year are indicated in Table 4. Reasons for the variation in egg numbers are unknown.

The number of eggs per cell of male and female broods is given in Table 5. Differences between sexes and years were statistically insignificant at 95%.

Table 4

Numbers of first, second, and third broods of eggs, larvae and pupae from nests of Bombus polaris at Lake Hazen, N.W.T., for 1967 and 1968.

	first brood (worker)		second brood (male)		third brood (queen)	
	N	Range	N	Range	N	Range
1967						
egg	2	16-17	8	4-34	8	8-23
larvae	6	14-17	7	4-23	8	2-18
pupae	8	13-17	5	2-15	5	2-6
1968						
egg	2	15-17	6	6-24	6	11-18
larvae	7	15-19	8	8-24	7	3-16
pupae	6	14-19	7	4-24	5	5-16

Table 5

The number of eggs per egg cell of B. polaris male and female broods per year at Lake Hazen, N.W.T.

	Male		Female	
	N	Range	N	Range
1967	21	2-13	18	4-17
1968	11	3-14	10	5-12

The ratio of the number of larvae of sexual forms to the number of workers in 1967 was 1.57 whereas in 1968 it was 1.53. A comparison of males with females within each nest places the ratio for 1967 at 2.0 males per female and for 1968 at 1.6 males per female.

Although the queens were successful in rearing almost all the first brood workers, they were less successful in the second and third broods. Of those nests studied during the entire seasons, 57.1% and 37.2% mortality occurred in the males and 62.5% and 41.0% mortality occurred in the queens in 1967 and 1968.

The time required for the development of each brood of B. polaris and stage of development given for each year are indicated in Table 6.

Discussion

Other species of Alpinobombus differ in brood composition and development from B. polaris and other members of other subgenera of Bombus. Hasselrot (1960) reported that only one batch of nine workers of B. balteatus developed before the sexual forms emerged in the nest. The developmental stages lasted 3 days for eggs of all castes, 8-12 days for larvae workers and 8-13 for larvae of sexuals, 6 1/2-12 days for pupae of workers, up to 23.5 days for queens and up to 13 days for males. Total developmental time was 18-30 days for workers, up to 40 days for queens, and up to 30 days for males. A comparison between B. balteatus, reported by Hobbs (1964a, b), and B. polaris follows in Table 7.

As members of Alpinobombus are the only bumblebees known to place all eggs in a single egg cell in the first brood, I consider this to be

Table 6

Duration of development in days of egg, larvae, and pupae of first, second, and third brood of Bombus polaris at Lake Hazen, N.W.T., 1967 and 1968.

	first brood (worker)		second brood (male)		third brood (queen)	
	N	Range	N	Range	N	Range
1967						
egg	5	3.5-4	7	3.5-4	7	3.5-4
larvae	9	7 -9	3	9 -11	4	7 -9
pupae	8	<u>7 -9</u>	3	<u>7 -11</u>	4	<u>9 -11</u>
Total		17.5-22		19.5-26		19.5-24
1968						
egg	1	3.5-4	3	3.5-4	2	3.5-4
larvae	3	7 -8	3	7 -9	2	6 -8
pupae	4	<u>6 -11</u>	4	<u>9 -14</u>	5	<u>9 -13</u>
Total		16.5-23		19.5-27		18.5-25

Table 7

Comparison between the composition and development of brood of B. balteatus and B. polaris (Data for B. balteatus after Hobbs 1964b)

<u>B. polaris</u>	<u>B. balteatus</u>
<u>First brood</u>	
-all eggs deposited vertically at at one time in a single egg cell	-not all eggs deposited at one time, but all vertical and in a single egg cell
-average no. of eggs in four broods 16.25 (range 15-17)	-average no. of eggs in eight broods 11 (range 7-21)
-average no. of larvae in 13 broods 15.9 (range 14-19)	-average no. of larvae in five broods 14 (range 12-15)
-larvae in curled position and collectively fed pollen pushed under the brood; "pocket-maker"	-similar
-last instar larvae fed individually pollen and honey	-similar
<u>Sexual brood</u>	
-eggs laid on same ridge of incubation groove were of different ages and caste	-eggs laid on same ridge of incubation groove were of different ages but same caste
-wax-pollen canopy covering larvae of adjacent cells was not extended to cover all larvae on the same ridge	-wax-pollen canopy covering larvae of adjacent cells was extended to cover all larvae on the same ridge

-bees were "pollen-storers"	-similar
-all stages of larval development collectively fed honey and pollen	-similar
-last instar larvae fed individually honey and pollen	-similar
-pupae development with males emerging before females	-similar
-only one brood of workers produced before males and queens	-sometimes more than one brood of workers produced before males and queens

one of the most important adaptations to arctic and alpine survival. By doing this the time required by the queen to construct egg cells, incubate the eggs, larvae, and pupae, and collectively feed the larvae is minimal.

Hobbs (1964a) discussed brood-rearing behavior in relation to phylogeny. Alpinobombus colonies are small, usually producing only one brood of workers before progressing to sexual production. Other subgenera with more southern members produce at least two worker broods. Even members of B. (Pyrobombus) sylvicola Kby. (= lapponicus Fab.), which produced nests in arctic Europe and Asia, Greenland and in Southern Alberta to elevations of over 7,200 feet, produced some colonies with more than 139 cocoons (Hobbs, 1967b). At the extreme, for a tropical species, B. medius Cress., Michener and LaBerge (1954) described a nest of 2183 offspring with no sexual development started.

The paucity of arctic worker bumblebees led Friese (1902, 1908, 1923a, b) and Friese and Wagner (1912) to suggest that arctic bumblebees are tending towards a solitary form of life. Sparre-Schneider (1894, 1898, 1906) also indicated a scarcity of workers of B. balteatus (= kirbyellus) and B. hyperboreus, and Richards (1931) has low ratios for the number of workers/female, based completely on museum specimens of arctic species.

Although Alpinobombus colonies have a low number of workers in comparison to colonies of other subgenera, I believe members belonging to Alpinobombus are not tending towards a solitary form of development. They are social in their brood-rearing behavior and have developed adaptations for survival in the arctic and alpine regions. Richards

(1931) did not state which females (spring or fall) were studied when he quoted his queen to worker ratios. If for B. polaris it was the number of spring females to number of workers produced then a more accurate ratio is 1:1.6 and if for fall female to workers then the ratio for 1967 is 1:3.03 and for 1968 1:1.76. These ratios are higher than the 0.8 which Richards (1931) proposes for this species. The ratio from museum specimens of B. polaris available was 6.89 workers per female. No doubt the ratios of Richards (1931) for the other species are of questionable significance. However, Cumber (1949a) and Richards (1946) found the larvae of sexual/worker ratio to vary from day to day in more populated nests. Frison (1927c) and Free (1955b) suggested the production of queens was brought about by a reduction in the larvae/worker ratio with the result that an increased amount of food became available per larvae.

Members of the subgenera studied by Hobbs (1964-1968) except sometimes B. (Subterraneobombus) appositus Cress., produced fewer workers in the first brood than members of Alpinobombus. Thus the worker/spring queen ratio is higher in the arctic and alpine species than in species of lower temperate forms. The number of eggs laid in the second and third broods of Alpinobombus polaris and probably the other related species was the same as those of succeeding worker and sexual egg cells of Bombus and Cullumanobombus and was greater than Subterraneobombus, Fervidobombus, Pyrobombus, and Bombias. Bombias is the only subgenus known where one egg per cell is laid in the second and succeeding broods (Hobbs, 1964a, 1965a). The high number of eggs per cell perhaps resulted from the brief favourable climatic period for brood rearing.

It is difficult to estimate the workers per fall female ratio for species of lower latitudes because of variations in worker brood numbers between nests and species, but generally this ratio is the same for temperate and alpine-arctic bumblebees. Total eggs laid in the first three broods of B. (Alpinobombus) polaris is higher than that of most of its lower latitude relatives, but because environmental factors restrict the total number of broods the seasonal egg production is less for the arctic species.

Mortality data are poor because not all second and third brood egg cells were opened to determine the maximum number of eggs laid. The artificial domicile colonies had lower mortalities than the natural colonies, presumably because of the insulating effects of the styrofoam top. Cumber (1949a) estimated at least 50% total mortality for bumblebees in general, and Brian (1951a) estimated mortality of B. (Agrobombus) agrorum Fab. based on all broods except the last for two years at 64 and 69 per cent.

Reasons for brood reduction at Lake Hazen were human interference, cannibalism, and lack of food. The latter is related to periods of unfavourable weather (about 4.0 ± 2.0 C, wind 8-12 mph. and complete cloud) during which workers had difficulty in foraging and the food supply within the colonies became depleted (i.e., honey pots less than 1/3 full and fresh moist pollen scarce). Under these conditions the workers demolished egg cups, eggs, removed first to last instar larvae thus reducing the population of the nest. This was presumably proportional to the amount of food being foraged. Food sources were also influenced by unfavourable weather as nectar secretion was probably reduced, stamens

became devoid of pollen, and the leaves and petals were blown off. I consider the feeding of either honey or pollen collectively to the second and third broods as an adaptation to unfavourable weather conditions.

Hasselrot (1960) reviewed the history of bumblebee brood development and nest temperature. The nest temperature values obtained for various nests of Bombus are similar (Hasselrot, 1960) and thus the rates of development are similar. Hasselrot's own mean values for all species, castes and broods were 3.4 days for the egg stage, 10.8 days for the larval stage, and 11.3 days for the pupal stage, a total of 24.5 days. Since then Hobbs (1965a, b, 1966a, b) estimated the total number of days required by queens to produce workers for B. (Bombias) nevadensis Cress. as 24-29 days, for B. (Cullumanobombus) rufocinctus Cress. as 17-27 days, for B. (Fervidobombus) californicus F. Sm. as 25-31 days, and for B. (Subterraneobombus) appositus Cress. as 21-25 days. Wójtowski (1963b) estimated that the developmental cycle of a B. terrestris colony took 128 days. This was four weeks shorter than that of B. agrorum. Variations exist between and within species records from different localities and by different authors and our knowledge on this subject is still far from sufficient.

The developmental times for colonies of B. polaris compare with those of other species of Bombus, and thus generalizations comparing lower latitude forms cannot be made. Variability of an individual brood group was in the larval and pupal stages of growth and was caused by irregular feeding and incubation by the queen and later workers. Larval position caused insufficient supply of food and resulted in smaller bees

with longer developmental times. Sladen (1912), Cumber (1949a), and Brian (1951a) have indicated the variation, in size of workers and brood developmental time, was caused by possible inherent differences, collective and competitive feeding and association of individuals of different instars. Hobbs (1965a, b, 1966a) relates the time required for development to the period of nest establishment, because those queens that established earliest required the longest time to rear workers, and queens that established latest the shortest time, this being related to the earlier cooler weather.

Yet bumblebees are one of the few arctic insect groups which utilize the majority of the biological active growth period at Lake Hazen. They were active soon after the first flowers bloomed to the first part of August when only a few flowers were present. The progression of brood development was parallel to the progression of the climate and plants. The relative lengths of the biologically active seasons may and do vary from year to year. Thus the most dramatic effects on bumblebees occurred at the termination of the season when food became scarce, because the flowers were producing seeds, and when the weather became more severe in progression to winter. Also the possibility that in some years the weather may be so bad as to reduce the ability of the queens to forage for food resulting in mortality of workers, males, and queens would have devastating effects on the population. These are dangers to arctic bumblebees during their brief developmental period. A species whose members have a long life cycle, especially if the length is not rigidly fixed, cannot be eradicated by the unduly harsh weather of a particular season, or even of a series of seasons (Downes, 1962, 1964, 1965).

However, the members of Alpinobombus probably do not belong to this latter category as do some butterflies, moths, and mosquitoes and have developed other adaptations to compensate. As stated, primary among these are the depositing of all eggs of the first brood in a single egg cell; and the method of feeding pollen collectively to all worker larvae, except the last instar of all broods which were fed individually a mixture of pollen and honey. Second and third brood larvae, except last instar were fed collectively a mixture of pollen and honey. If these physiological and morphological developmental features of the brood-rearing behavior had not developed, this species would not survive in the arctic regions.

Flight activity

Introduction

Flight activity is a sensitive indicator of foraging conditions in the field, and of the ability of colonies to exploit available food sources. The rate of food acquisition strongly influences the health, reproductive capacity, and tempo of most activities within colonies (Gary, 1967). Although Gary (1967) studied honey bee flight activity, the same principles are applied to the flight activity of bumblebees. The purposes of this study were to characterize the weather conditions affecting the foraging of arctic bumblebees, the adaptations of the bees to the weather conditions, the frequency of flight per 24 hours, and the type of food (pollen or nectar) exploited. The pollination adaptations and period of flower visitation are described in a following section.

The effect of weather and general climatic conditions on bumblebee flight (Løken, 1949, 1954, Hasselrot, 1960), especially in the arctic (Jacobson, 1898 in Friese, 1904, 1908, 1923a, b, and Friese and Wagner, 1912, and Johansen and Nielsen, 1910, Sladen, 1919, Frison, 1919, Longstaff, 1932, Bruggeman, 1953, Freuchen and Salomonsen, 1958, Savile, 1959, Gavrilok, 1961, Downes, 1964, Hocking and Sharplin, 1964, and Milliron and Oliver, 1966), where 24 hours of light during the summer has an influence on the maximum flight hours and frequency from the nest is important. The foraging behavior exploited (Sladen, 1912, Brian, 1952, 1954, Free, 1955b, c, Taniguchi, 1955) and the social facilitation at the nest entrance (Frison, 1930c, Blackith, 1957) are influenced by

the weather conditions. Adaptations, such as large size, hairiness, and tendency to melanism (Sladen, 1918, Frison, 1919) and some physiological factors (Strelnikov, 1931, Bertram, 1935, Parry, 1951, Digby, 1955, Church, 1960a, b) affecting the foraging in cooler weather are discussed.

Materials and methods

My investigations of the traffic through the nest entrance were carried out in the following manner. In 1968 24 hour observations were made every six days for 36 days at an artificial domicile. These six observations were made at the following stages of development: first brood mid-larval, first brood early-pupal and second brood egg, first brood emergence second brood late-larval early pupal third brood egg, second brood late-pupal third brood mid-larval, second brood early emergence third brood pupal, and third brood early emergence late-pupal development. Six supporting observations from a natural nest at unspecified intervals of hour and day and occasional flight activity observations at an artificial domicile in 1967 were also made. The brood composition and population of the nests were taken the day before each observation. Thus, the flight activity of the nest at major brood developmental period was characterized.

Flight was observed from a seated position at a distance far enough from a nest so as not to disturb orientation and yet near enough to recognize the caste (queen or worker) and presence or absence of pollen on legs. When reference is made to a 'pollen load' or 'pollen-gathering' it is assumed that the bee was often also carrying nectar (Brian, 1952,

Free, 1955c). The terms 'nectar load' and 'nectar-gatherer' are only used when the forager in question had not been gathering pollen (Free, 1955c).

The time, the caste, incoming or outgoing, and the presence or absence of pollen on the hind legs of incoming bees was noted for each bee. The air temperature was taken with a thermistor-thermometer probe and later with a dial thermometer, the wind velocity in mph and the wind directions were estimated with a portable anemometer floating ball-type. All were taken at a height of 20-30 cm near the nest. The anemometer readings are estimates because the 0-2 mph range was absent from the recording scale and because the plastic ball fluctuated slightly at most velocities. The cloud cover was estimated by visual observation. Several readings of the air temperature, wind velocity and direction, and several estimates of the cloud cover throughout each hour of observations were averaged to increase the reliability of the data. The solar altitude at four times of the day was taken from Corbet (1966).

For each bee observed other than at the nest entrance the following notes were taken: species, caste or sex, time, air temperature, wind direction and velocity at height of flight, cloud cover, and flying height above the ground.

Frequency of food collecting at the nest entrance

Two integral components affecting the flight activity were the responses of foraging bees to intranest stimuli and to meteorological conditions. Various combinations of light, temperature, wind, and humidity affected bumblebee flight. Thus, a summary of the diel periodicities of

weather factors near the ground at Lake Hazen (Corbet, 1966, 1967b) in Table 8 are considered and might be sufficient to bring about biological periodicities in flight. Jackson (1959b) reported an average wind velocity at one foot above the ground of about 75% of that at 41 feet and that for 76% of the observations the average wind velocity from 1 June to 2 August was very low at 5 mph or less. The predominant wind direction was NE, along the Lake Hazen trough (Jackson, 1959b, Corbet, 1966, 1967b) followed by ENE, E, NNE (Corbet, 1966). Cloud cover did not exhibit diel periodicity, but a tendency was noted for opacity to increase slightly between 1300 and 2200 hours (Corbet, 1966).

Many of the diel fluctuations were obscured by weather trends persisting longer than a day, such as barometric pressure, wind velocity, and cloud cover. The most regular are those resulting directly from solar radiation at or near the soil surface (Corbet, 1966).

The frequency of flight and the number of pollen and nectar loads collected on various days by foragers of a B. polaris artificial colony are shown in Figs. 17-22 and for a natural nest are shown in Figs. 23-26.

Before the workers emerged the queen (Fig. 17) flew at all hours of the day and night, with approximately equal frequency, collecting more pollen than nectar to feed the first brood larvae. The queen was away from the nest approximately 30 minutes on 20 foraging trips. After each forage she deposited the pollen into the pollen pocket(s) and/or honey pot(s) and incubated the brood to a temperature comparable to that before her forage. On four occasions (Fig. 17, 1017, 1154; Fig. 18, 1234, 0145) the queen remained in the nest a longer time. Perhaps she was compensating for the minimal temperature losses which may have affected

Table 8

Time of Maximum and minimum diel periodicities of weather factors near the ground at Lake Hazen, N.W.T. (after Corbet, 1966).

Weather factor	Maximum	Minimum
solar altitude and short wave radiation	1000-1600	2200-0200
soil-surface temperature	1300-1600	0100-0300
Stevenson screen temperature	1300-1900	0100-0700
relative humidity	0100-0700	1300-1900
wind velocity (at 41 feet)	1900-2200	1600-1900

the normal first brood larval development. When the first brood were in the early pupal stage (Fig. 18) the queen collected pollen, but the frequency of her flight was more irregular than during larval development.

The climax of worker foraging activity occurred from about July 6 to about July 12 because of the maximum nutritional requirements of the second and third brood larval period (Fig. 19 and Fig. 20, respectively). These larvae were fed mixtures of pollen and nectar. The proportions of pollen loads to nectar loads collected by foragers for these two days were 2.20:1 and 1.14:1, respectively. Thus, there is perhaps a difference in the pollen to nectar proportions fed to the second and third brood larvae. Nectar-gathering reached a peak during 1200 to 1600 hours, whereas, the amount of pollen foraged remained nearly the same throughout July 6. But on July 12, the pollen-gathering peaked during 1000 to 1400 hours and nectar-gathering was proportionately higher most other times. Collectively nectar- and pollen-gathering occurred between 1200 and 1600 hours on July 6 and between 0900 and 1500 hours on July 12. The highest value for the number of worker bumblebees (37) passing through the nest entrance in one hour was counted at about 1400 hours on July 6. On July 12 workers flew until 2330 and no foragers spent the night away from the nest.

During the second brood early emergence and third brood pupal periods (Fig. 21), the queen and workers foraged primarily for nectar. This corresponds to the increase in the number of honey pots, to the feeding of second and third brood larvae quantities of honey, and to

the feeding of newly emerged adult males. Males immediately after emergence were observed taking honey from one of the many honey pots. The queen flew 24 hours a day, but at infrequent intervals. She remained away from the nest for longer periods than during the period of larval sexual development and eventually departed just after the first males emerged.

The peak flight activity for workers was not noticeable, but perhaps was greatest between 1000 and 1700 hours. Flight activity was reduced until past 2400 hours, but was not, as yet, a complete 24 hour activity. The nutritional requirements of the nest were reduced and this influenced the peak flight activity. The population of the nest was also reduced as some foraging workers had died. Brian (1952) reported that on the average, 29% of the bees in the nests she studied died every 5 days.

On July 24 (Fig. 22), the newly emerged third brood queens and some workers were observed in flight at the nest entrance. All collected only nectar. The new queens and workers flew throughout the 24 hour period with no definite peak in activity. The nutritional requirements of the nest were low as the development of the colony was completed. Nectar-gathering was necessary for maintenance of the sexual and worker forms and for preservation of a sufficiently high nest temperature for emergence of the remaining fall queens. Once males had left the nest they did not return, thus did not forage for the nest. Two males were observed leaving, at 0838 and 0922.

The flight activity at the natural nest (Figs. 23-26) was similar to the flight activity at the artificial domicile and any variations (i.e., foraging and brood populations, nutritional requirements) are in

the respective nest developments. However, the queen in the natural nest foraged longer than the artificial domicile queen.

On July 12, 1967, at an artificial nest, the peak of activity was from 1400 to 1800 hours with 57 of 95 workers observed bringing pollen to the nest. The queen and workers did not fly throughout a 24 hour period on that day. Subsequent flight activity observations had ceased by 2200 hours, and by July 19 the flight activity had ceased before 0100 hours.

Weather conditions affected the queen little while she provided for the nest (Fig. 17-18). But, she remained within the nest, presumably incubating, during light snow storms on June 17, 1967, and on June 29, 1968. The air temperature at 30 cm above the nest on June 17 was -0.5 C and on June 29 was 4.5 C. Internal nest temperature on June 29 in an artificial nest was 27.0 C and in a natural nest was 19.5 C.

Generally, cloud cover, wind direction, and wind velocity had little influence on the frequency of worker flight activity from the nest entrance. But, on July 12, 1967, a mean wind velocity from 0815 to 2230 at a height of 15 cm above the ground was 12 (range 7-18) mph from the SE. This wind caused approaching workers to land or to be blown to the ground. On the ground they walked or remained behind the protection of Salix and Saxifraga clumps before continuing to the nest entrance. Without orientation circles the workers always flew into the wind while leaving and returning to the nest when the wind velocity was above 8 mph. Unusually low wind velocities did not affect flight activity or foraging, but higher velocities affected foraging and probably resulted in some brood reduction. Brian (1952) believed 'bad' weather, notably wind,

probably shortened the adult bee's life. Light showers on July 24 (Fig. 22) reduced flight activity slightly.

The climatic factors affecting any periodic properties of circadian cycles are temperature and sky illumination (Marler and Hamilton, 1967), the latter depending mainly on the theoretical sun's altitude. During that part of the season when the workers were flying, the maximum solar altitude varied by three degrees, but within a day the variation between maximum (solar noon) and minimum (solar midnight) altitude was about 16 degrees. The bumblebee workers did not begin foraging in the morning until the sun was at least 18 degrees above the theoretical horizon. Yet the workers did not cease foraging when the altitude of the sun was below 18 degrees, but continued foraging for longer periods each day until by July 24 they were flying a complete 24 hours. Thus towards the end of the season the 24 hours of illumination influenced any existing periodic properties.

Increases starting about 9-10 C in the diel fluctuations of air temperature, are correlated to increase in the frequency of flight activity and the maximum diel air temperature corresponded closely to the peak flight activity.

Throughout a season the tendency for the rate of food acquisition to shift from pollen-gathering to nectar-gathering and the tendency to shift the maximum number of foraging hours each day to 24 are behavioral responses to the prevailing weather conditions, to food availability, and to the nutritional requirements of the brood.

Explanation of symbols used in Figs. 17-26 in the flight activity and nest temperature of B. polaris, 1968, at Lake Hazen, N.W.T.

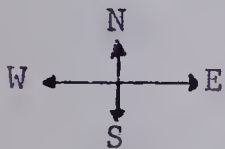
time = hours

cloud cover

clear	0/8	
slightly cloudy	2/8	
fairly cloudy	4/8	
rather cloudy	6/8	
overcast	8/8	

rain = .

wind direction



velocity in mph



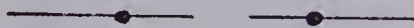
variable

angle of sun attained from Corbet (1966)

air temperature



artificial domicile temperature



nest temperature



flight activity

(worker)

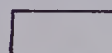


without pollen loads

with pollen loads

↑ outgoing ↑ incoming

(queen)



without pollen load

with pollen load

length of box indicates

duration of forage

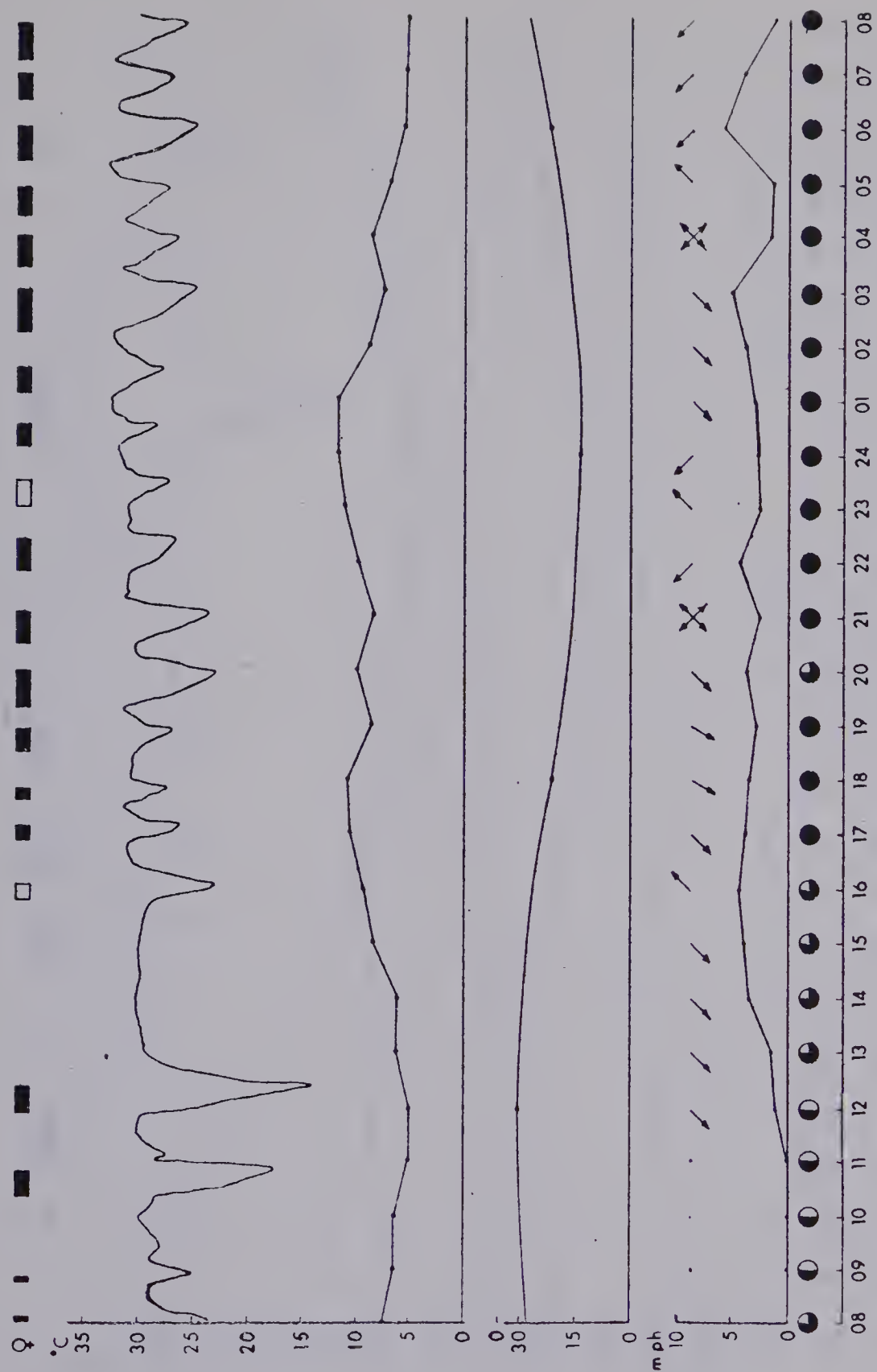


Fig. 17 Flight activity and nest temperature, June 23-24, one queen, 17 first brood larvae

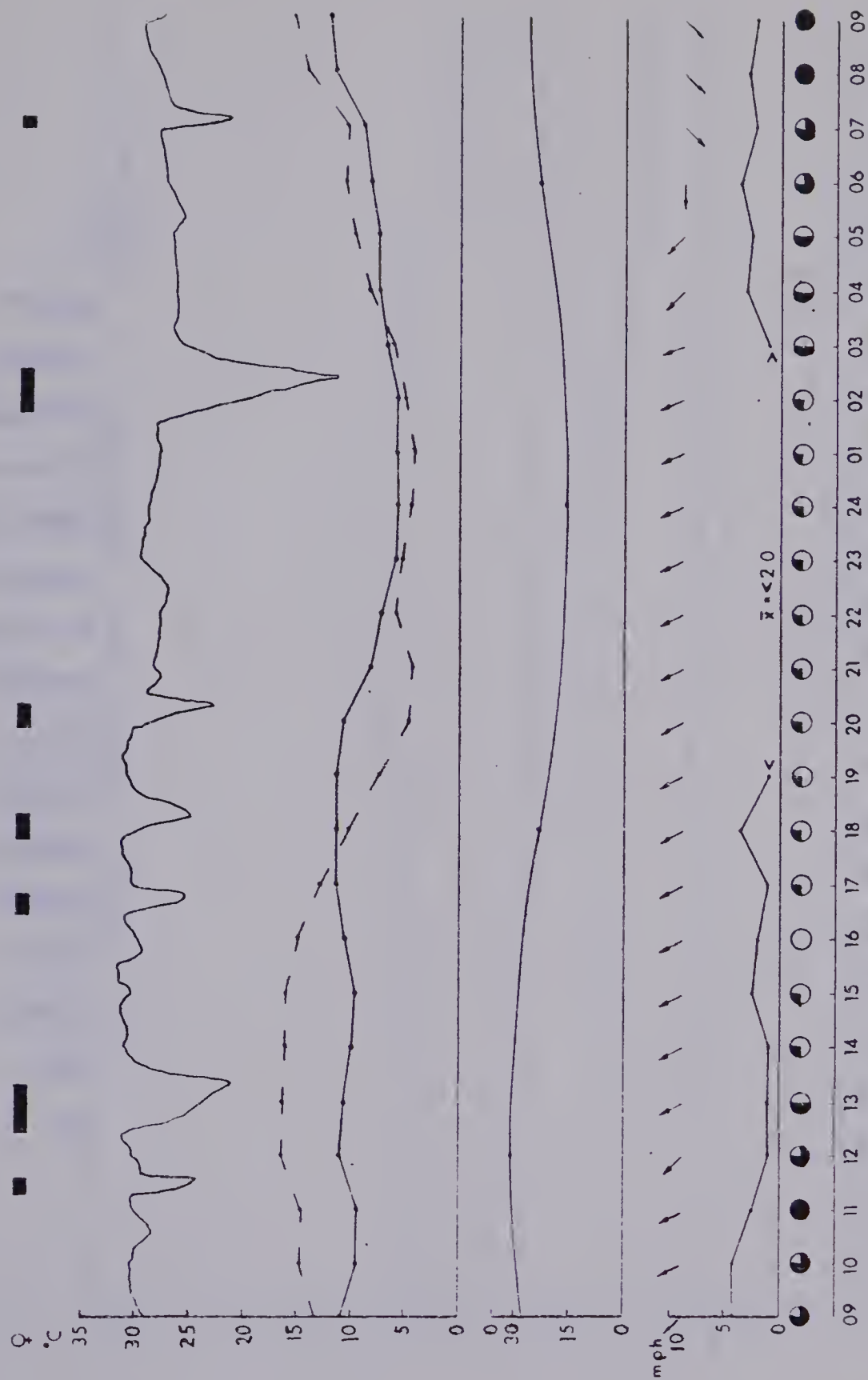
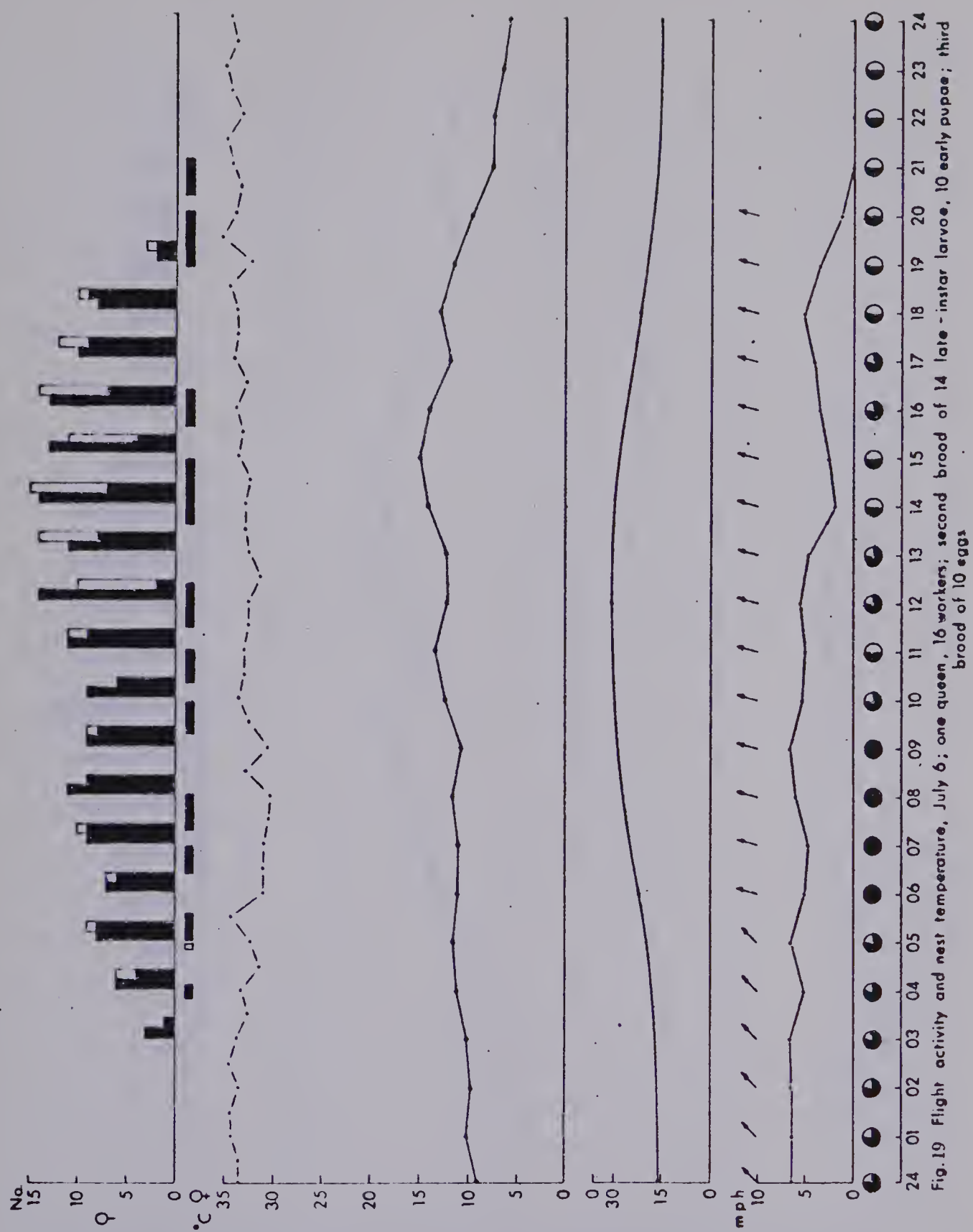
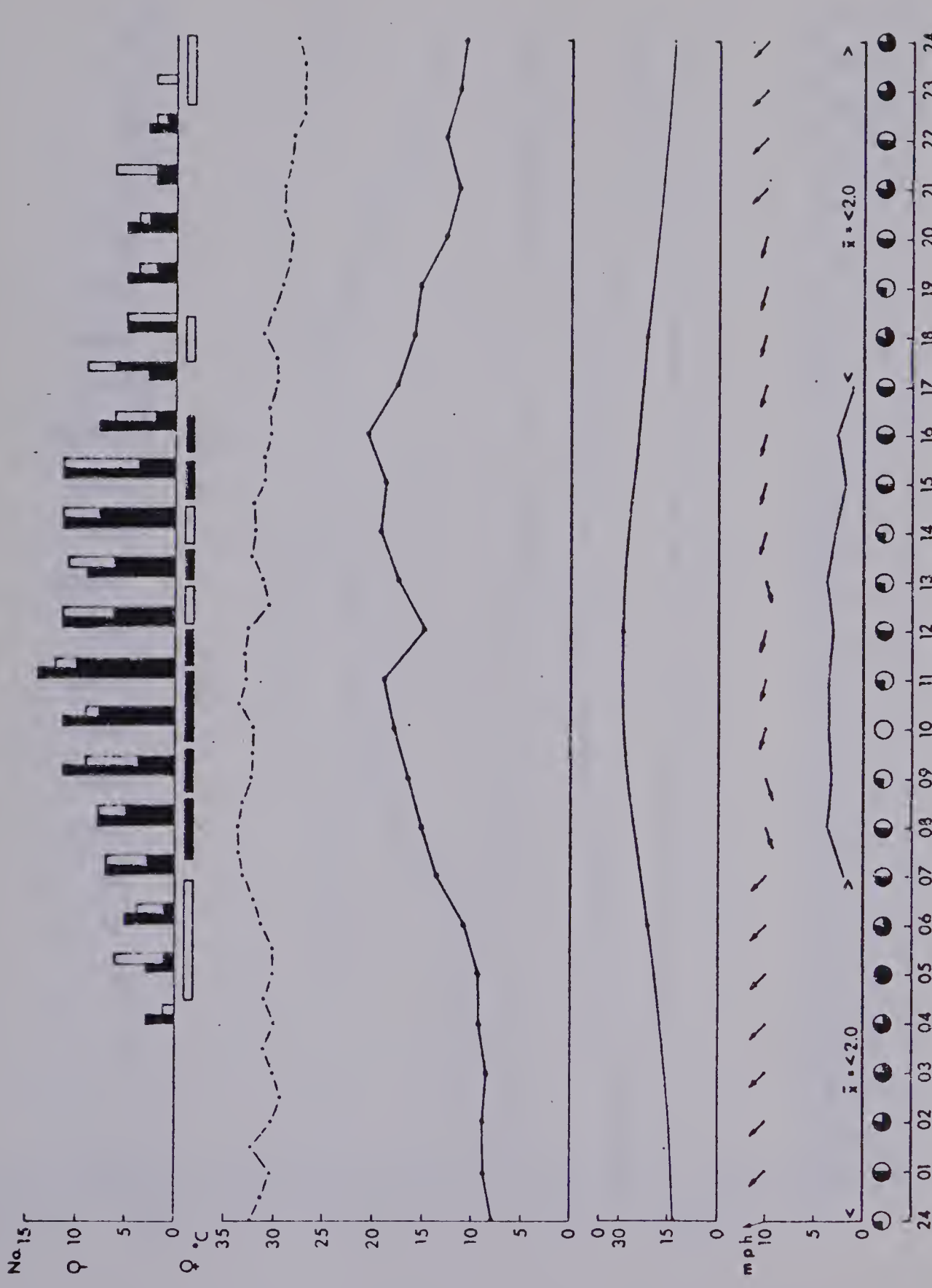


Fig. 18 Flight activity and nest temperature, June 30 - July 1; one queen, 17 first brood pupae, 10 second brood eggs





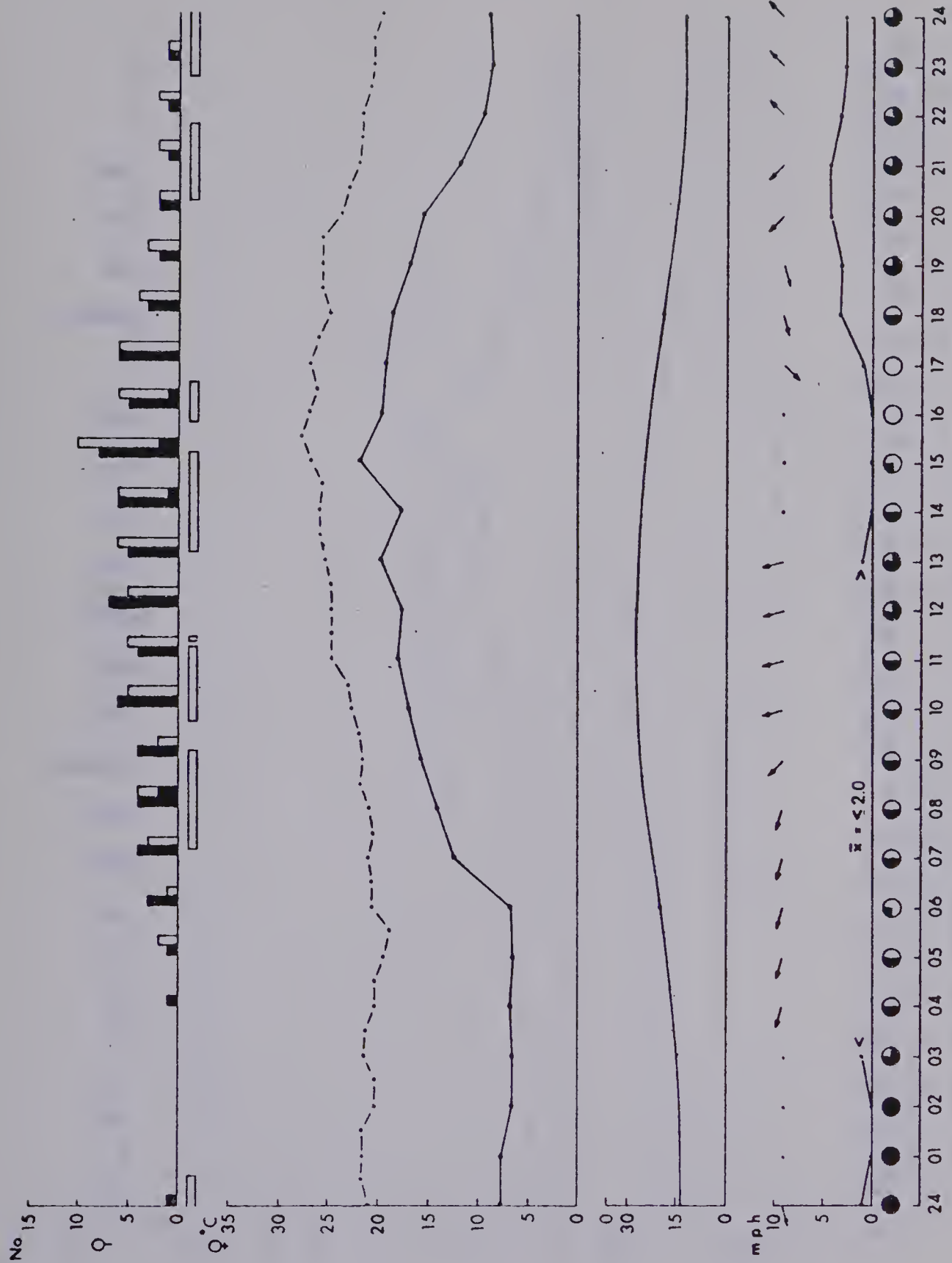


Fig 21 Flight activity and nest temperature, July 18; one queen, 10 workers; 3 males; second brood 21 late-pupal; third brood 6 eggs, 10 pupae

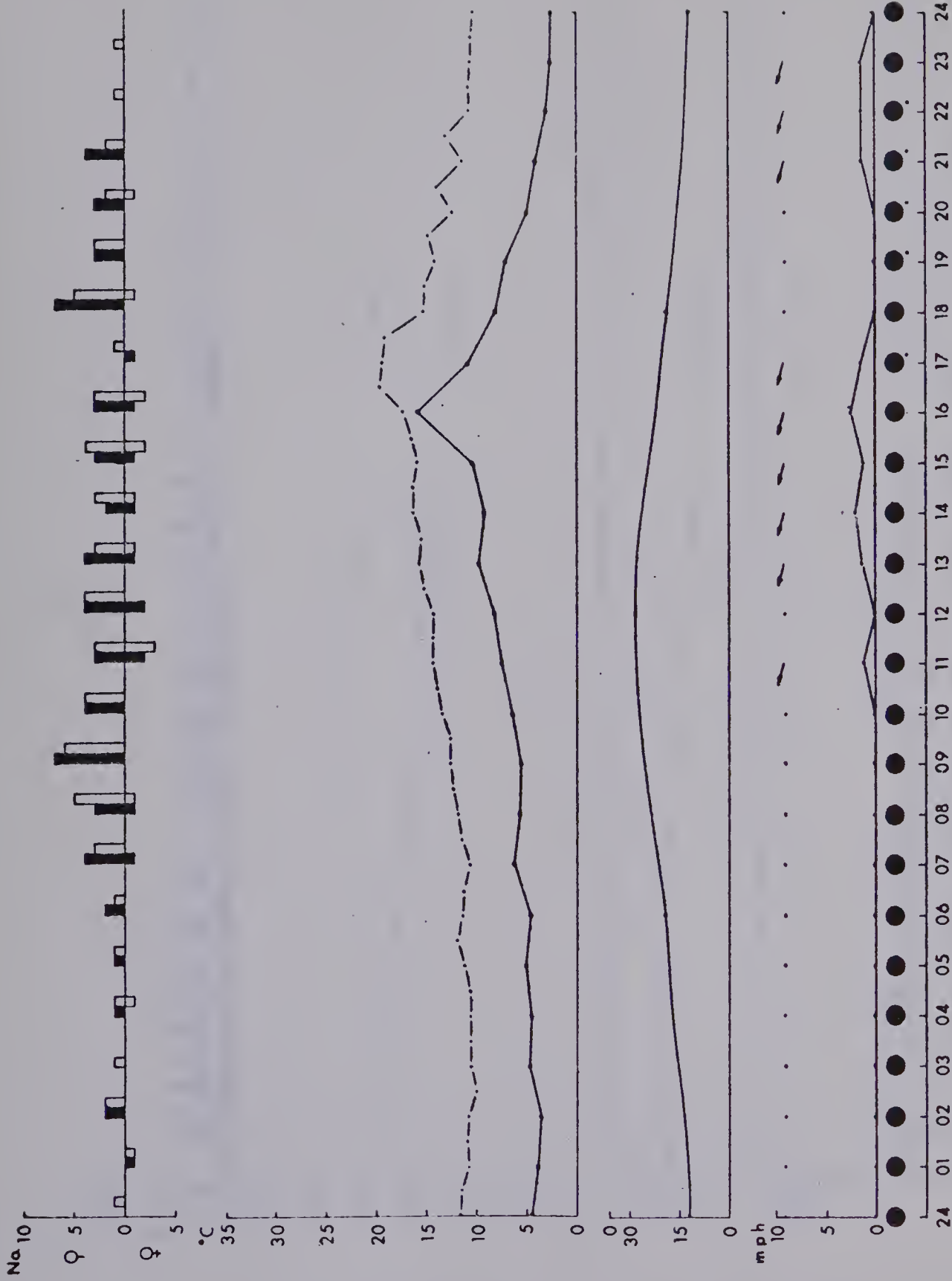


Fig. 22 Flight activity and nest temperature, July 24; 9 workers; 5 fallqueens, 2 males; third brood 5 late - pupal

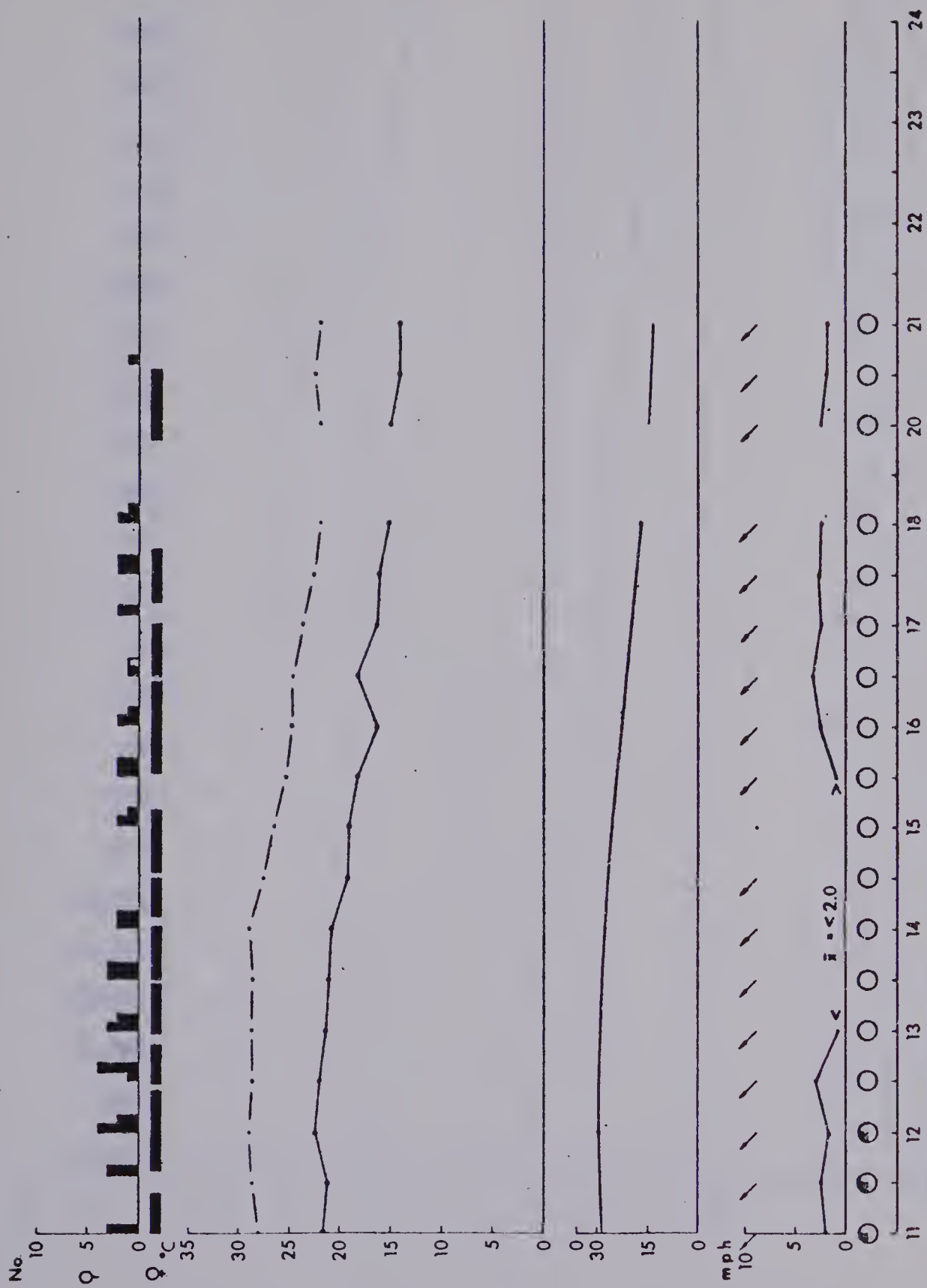
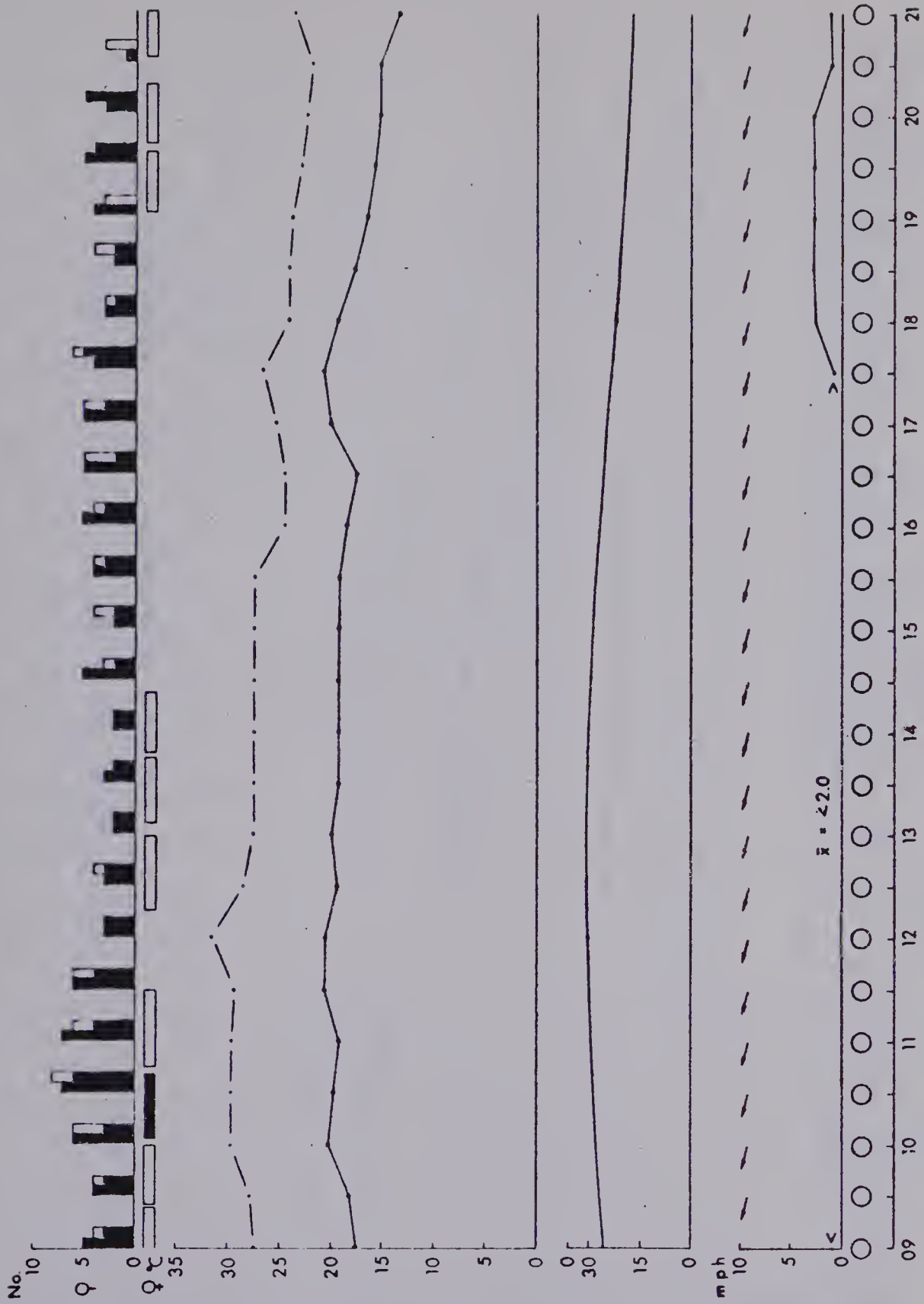


Fig. 23 Flight activity and nest temperature, July 9; one queen 14 workers



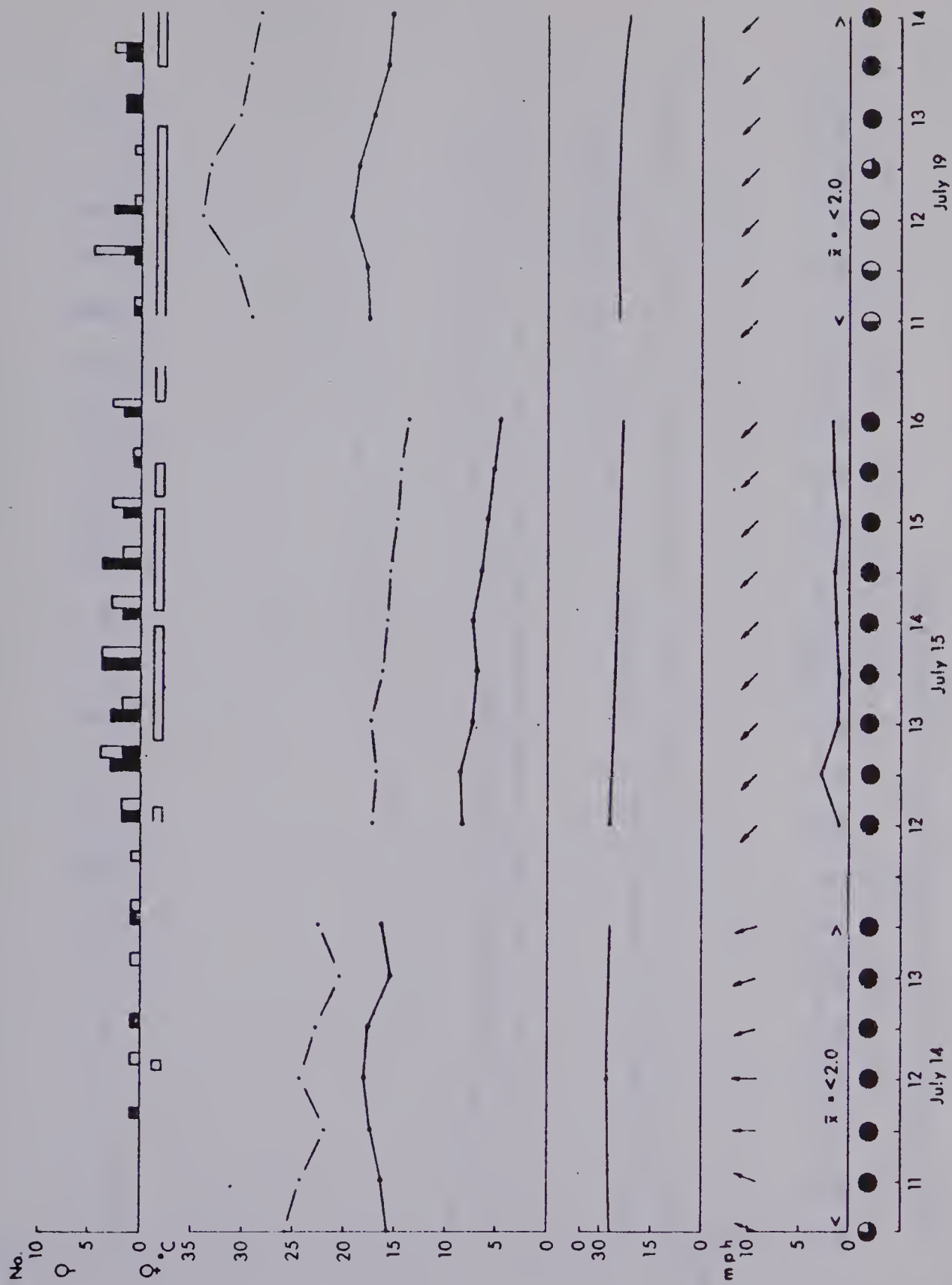


Fig. 25 Flight activity and nest temperature, July 14, 15, 19; one queen, 10 workers

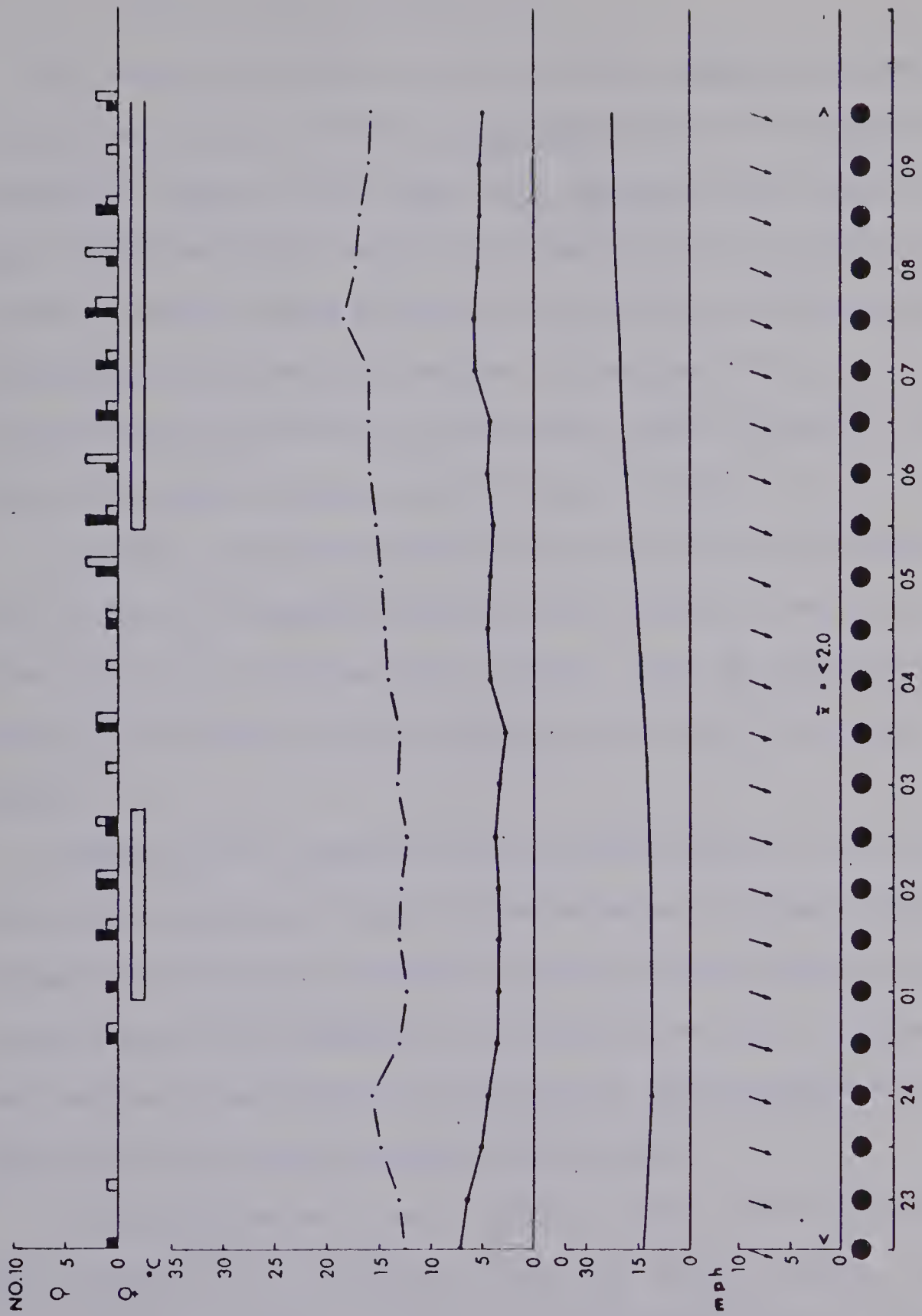


Fig. 26 Flight activity and nest temperature July 21; one queen, 8 workers

Flight in the foraging area

The duration of flight activity of the B. polaris workers, males and fall queens, and of the B. hyperboreus males and fall queens is presented in Table 9. The flight of B. polaris workers began 32 and 18 days in 1967 and 1968, respectively after the first B. polaris queens had been observed flying and was one and one day in 1967 and 1968, respectively after the first workers had emerged from the brood cocoons. Although flying conditions were favourable until mid-August, I did not observe any workers foraging after the given dates.

Generally the flight of bees at a distance from the entrance was more difficult to estimate, because on any one day as few as two or three or as many as 66 bees were observed. Thus the nest entrance flight activity was a more sensitive indicator of foraging conditions in the field.

Bumblebees were observed flying in those habitats or in close proximity to those habitats where natural nests were located. Thus, the distance that foragers travelled from the nest was probably limited. In fact, one worker foraged at a distance of less than 10 meters from the nest and one queen foraged for nectar of S. oppositifolia flowers at a distance of less than 100 meters from her nest.

As low temperatures tend to restrict flight and wind disrupts the warm air produced by insolation at the soil surface (Downes, 1965), the height of flying above the soil and the corresponding air temperature are considered important. The profile of air temperature above the soil surface was measured at a sandy-clay soil site by a thermistor-thermometer air probe at 1400 hours four times during the summer of 1968 (June 30,

July 5, July 15, July 31) at heights of 0, 5, 10, 15, 20, 30, 40, 50, 75, 100, 150, 200 cm above the soil. The profiles of the incoming-radiation type (Geiger, 1965), resembled those recorded at Lake Hazen by Powell (1961) and Corbet (1967b) on different days of the season (Fig. 27). In all cases an abrupt increase occurred within 5 cm of the ground. The same patterns persisted on completely cloudy and windy days (July 15, July 31) as on nearly clear calm days (June 30 and July 5). On all four days the air temperature at the estimated maximum height of flying of queens and workers was about 7.75 to 10.25 C, even though the temperature range near the ground was about 10.0 C.

As for a minimum temperature, Bertram (1935) found experimentally that 5 C (41 F) was the temperature at which B. polaris individuals became inactive and that 9.5 C (49 F) was the temperature that the bee could no longer retain its normal or effective activity, I have observed four queens foraging for nectar from S. oppositifolia at -1.7 C (29 F). Gavrilok (1961) found that the bees did not work in temperatures below 4-5 C, or in frosty fog. The flying height temperature for only those bees measured for both seasons indicates that the bees flew most often at temperatures between 7-10 C, although early in the season (1967) the queens flew actively at a temperature between 1.7 and 4.4 C.

Discussion

Nutritional requirements, various sounds, odours, and other stimuli originating within the nest affect flight activity. Measurements of honey bee flight at the nest entrance permit a rapid evaluation of the relative effects of intra-nest stimuli (Gary, 1967). These same principles

Table 9

Duration of flight activity of castes and sexes of B. polaris and B. hyperboreus at Lake Hazen, N.W.T., 1967 and 1968

caste or sex	duration of flight activity	
	1967	1968
<u>B. polaris</u>		
workers	June 27 to August 10	June 2 to August 5
fall queens	July 21 to August 7	July 23 to August 3
males	July 16 to August 10	July 21 to August 5
<u>B. hyperboreus</u>		
fall queens	July 24 to August 6	July 24 to August 4
males	July 19 to August 6	July 23 to August 6

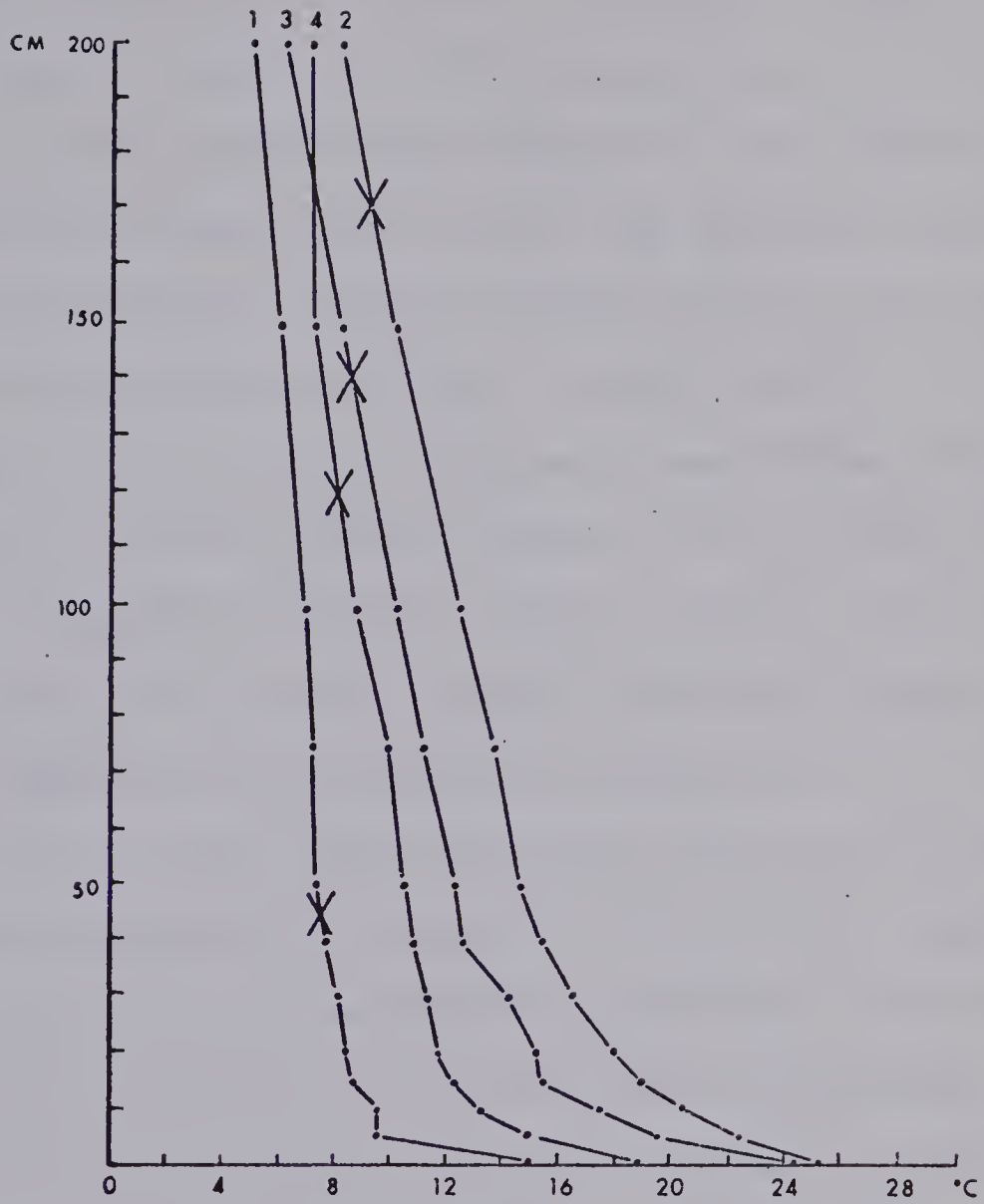


FIG.27 PROFILE OF AIR TEMPERATURE ON 1. JUNE 30, 2. JUNE 5, 3. JULY 15, AND 4. JULY 31; X MARKS THE ESTIMATED HEIGHT OF FLIGHT OF QUEEN AND WORKERS ON THOSE DAYS.

apply to bumblebee colonies. The responses of foraging bees to various combinations of meteorological conditions are just as important in the arctic as elsewhere and are as numerous and complex as those of the intra-nest stimuli. However, one factor predominates at these high latitudes; the daily range of light intensity in clear weather is less than the difference between night and day, and insects are unable to use the 24 hour rhythm either to control activity directly or for the uniform setting of an endogenous cycle (Corbet in Downes, 1965). In fact shifts in the flight activity occurred. The queens ceased flying throughout 24 hours when the workers commenced foraging, only to resume again near the end of the season. The workers gradually increased the daily duration of foraging until at the season's end they were flying throughout the 24 hours. When the colony required the maximum amount of food during the second and third brood larval development, the queen and workers did not fly throughout the 24 hour period, Frison (1919), Longstaff (1932), Freuchen and Salomonsen (1958), Downes (1964), Hocking and Sharplin (1964), and Milliron and Oliver (1966) notwithstanding. However, I believe the workers, shortly after emergence, tended to take their clues for a 24 hour rhythm from the height and position of the sun. Hocking and Sharplin (1964) stated that the activity curve for honey bees was synchronized with Hazen solar time and unlikely to be due to temperature, since at this latitude the difference between mean maximum and mean minimum temperature during the summer months is less than 5 C. The resulting shift of gradually increasing the daily duration of flight activity in response to the 24 hours of light is an important response to the meteorological conditions. This response may be classified

as an adaptation to the arctic conditions. Although not statistically tested, other meteorological conditions, such as low air temperature, wind direction and wind velocity, cloud cover, and humidity were of less importance to the frequency of flight.

Agreeing with Free (1955a) my results indicate that the type of food collected (pollen or nectar) was determined mainly by the brood's nutritional requirements. These nutritional requirements depended on the nature and amount of food stores in a colony and especially on the presence or age of larvae in the brood. Also the collection of food by arctic bumblebees follows the characteristics of lower latitude forms. The number of nectar loads and pollen loads collected at various times of the day by foragers and the proportion of pollen to nectar loads shifted gradually from near complete pollen-gathering during larval development to nectar-gathering in pupal development. Free (1955c) found the proportion of pollen loads to nectar loads increased during the day and he (1955a) reported that the foragers only collected pollen when the carbohydrate stores of their colony had reached a certain minimum level. However, Hasselrot (1960) reports no clear tendency to a forenoon or afternoon dominance in the pollen-gathering on separate days. I believe the variation of the proportions may be a means of indicating the stage of colony development.

The flight data, lead me to believe that the long shaggy hair and large body size, especially of the Alpinobombus queens, are special adaptations to alpine and arctic conditions. These bees probably develop considerable heat from the activity of the flight muscles, as other bees do (Newport, 1837, Hasselrot, 1960), and their shaggy hair enables them

to keep active in low temperatures (Sladen, 1919, Friese, 1923a). Church (1960b) has shown experimentally that bumblebee hair provides a well-marked and fairly consistent amount of insulation. The size of the insect and the density of the coat are more important than the length of the hair, during flight, though they seem to be of negligible value when at rest (Church, 1960b).

I agree with Sladen (1919) that arctic bumblebees show pronounced melanism and that members of the species B. (Alpinobombus) balteatus, B. (Pyrobombus) melanopygus Nyl., B. (P.) mixtus Cress., B. (P.) sitkensis Nyl., B. (P.) sylvicola Kby. of the Boreal Cordilleran transition zone of Alberta (Hobbs, 1967b) also have a tendency to melanism. This unusually dark coloration, generally rare in the North American bumblebee fauna (Sladen, 1919), increases absorption of solar radiation. This ability to be warmed by solar radiation would increase with the reduced size in workers because of the increase in the ratio of area to volume (Downes, 1962). Strelnikov (1931) and Parry (1951) believe morphological factors such as shape, color, and orientation determine the temperatures of the bodies of insects in sunshine. Digby (1953), however, who examined the temperature excess of insects in sunshine, found the effects of color on temperature excess was slight. Also the temperature rise by flight activity was not additive to temperature rise from radiation because it was associated with extra cooling, and Church (1960b) estimated the heat loss by convection from the surface of the pterothorax of a bee was 60-80% of the total losses.

Thus the large hairy appearance and dark coloration are factors which allow the bumblebees to be warmed by solar radiation and the relatively

low flying height suggested that the bees attain body warmth from the radiation reflected from the soil.

Nest Temperature

Introduction

Bumblebees, like some other social Hymenoptera, are capable of partly regulating their body temperatures independently of external air temperatures, and singly or collectively can maintain a nest temperature for a certain period of time. A study of the temperature relations of arctic bumblebee colonies at various stages of development was made to estimate the bumblebee brood temperatures. The effect of arctic climatic conditions on the brood temperature and a comparison between the artificial domicile and natural nest temperatures is discussed.

Data on the meteorological conditions and diel periodicities that may affect brood temperatures were presented in the flight activity section. Previous investigations of temperatures in bumblebee nests were by Himmer (1933), Nielsen (1938), Hasselrot (1960), and Wójtowski (1963a, b). I followed the three nest temperature periods of Hasselrot (1960). Newport (1837), Plath (1934), Cumber (1949a), and Brian (1952) have also measured the nest temperature, but these investigations have only reported the temperature of colonies at one particular stage of development. Fye and Medler (1954c) gave data on the temperature on different occasions in bumblebee nests in domiciles of different construction and insulation, and Hobbs, Nummi and Virostek (1962) investigated control measures of high temperature in above-ground artificial domiciles. Newport (1837), Sladen (1912), Free and Butler (1959), and Hasselrot (1960) reported on the heat generation and temperatures regulation in the nest by the body temperature of the bees.

Materials and methods

My measurements of brood temperature were made at the same time as my flight activity investigations at the nest entrance. I assumed the weather conditions influenced equally the nest temperature and flight activity. Some of the brood temperatures were taken with surface thermistor-thermometer probes which were placed under the first brood (Fig. 10) as near to the center of the brood as possible. After July 6, the brood temperatures within each nest were recorded with a dial thermometer as the thermistor-thermometer wiring was damaged. The recording instruments gave comparable results. Several readings of the nest temperature were taken each hour. The brood temperatures while the queen was foraging were taken at one to two minute intervals to characterize the fluctuations and the dependence on the queen of the first brood for incubation temperature.

Results

The temperature curves obtained for the artificial domicile nest (Figs. 17-22) and for the natural nest (Figs. 23-26), in their variation reflect the general development and well-being of the bumblebee colonies and thus, conversely, are a convenient and reliable method for determining the latter (Hasselrot, 1960).

During the period when the queen was alone (Figs. 17-18) incubating the brood, variations in nest temperature prevailed. These variations were numerous during first brood larval development (Fig. 17) and were related to the foraging of the queen. When she departed there was a brief period before the nest temperature started to decrease. On 20

occasions (Fig. 17) and at different air temperatures, the nest temperature decreased 0.22 C per minute while she was foraging. Similarly, when the queen returned a brief period occurred before the nest temperature started to increase, presumably while she deposits the collected pollen and/or nectar. Rate of increase was 0.43 C per minute and on the average 14.5 minutes elapsed before the former temperature was attained. Thus the queen through incubation increased the brood larval temperature twice as fast as it decreased. On seven occasions while the queen was foraging during first brood pupal development the nest temperature decreased 0.30 C per minute and when she returned the temperature increased at the rate of 0.27 C per minute and on the average 22 minutes elapsed before the former nest temperature was attained.

As indicated in the flight activity data, the queen remained in the nest (Fig. 17, 1017, 1154; Fig. 18, 1234, 0145) a longer time than she did between previous forages and compensated for earlier temperature losses. When these lengthy compensations occurred the nest temperature was as low as or lower than 21 C which may be the minimum temperature for normal first brood larval and pupal development. During this stage of nest development maximum nest temperatures are related to the higher air temperatures, but not to the maximum diel temperature which occurred between 1300 and 1600 hours (Corbet, 1966, 1967b). The difference between nest temperature and air temperature was 19 to 22 C. The minimum nest temperatures while the queen was in the nest are related to the minimum air temperatures and the difference between the two was 20 to 24 C. Hasselrot (1960) termed this the period of instability and variability of the nest temperature as the period of upbuilding.

During the next period (Fig. 19, 20), the period of equilibrium (Hasselrot, 1960), the temperature was generally high and even and varied only slightly. The variations for the complete day, July 6 (Fig. 19), were between 30 to 35 C and for July 12 (Fig. 20) were between 27 to 33 C. The nest temperature was 18 to 24 C higher than the outside temperature. The tendency for the nest temperature to vary in accordance with the variations in the external temperature was not noted in the artificial domicile at this stage of brood development.

During the period of decline (Hasselrot, 1960), (Figs. 21, 22) gradual decreases and variations with the outside temperature prevailed. Nest temperature variations for the complete day, July 18 (Fig. 21), were between 19 and 28 C with the maximum nest temperature 5 to 7 C warmer than the maximum air temperature and the minimum nest temperature 13 C warmer than the minimum air temperature. Nest temperature variations for the complete day, July 24 (Fig. 22), were between 10 and 20 C and were in close agreement (5 to 8 C difference) with the air temperature. As the air temperature increased and decreased the nest temperature increased and decreased.

The external air temperature was more influential in regulating the natural nest temperature (Figs. 23-26) than it was in regulating temperatures of the artificial domicile nest. Small variations in the air temperature resulted in corresponding variations in the natural nest temperature, even if the nest temperature was 7 C or more warmer. As shown on two adjacent days, July 14 and 15 (Fig. 25), the day with lower air temperatures by 7 to 10 C also had lower nest temperatures.

In addition to those climatic conditions resulting directly from solar radiation, the other climatic factors had more of an influence on the natural nest than the artificial domicile nest. With light snow and rain, and air temperature of 4.5 C, the natural nest temperature was 19.5 C; in comparison the artificial domicile nest temperature was always lower than was the temperature of the artificial domicile nest.

Data indicating the insulating effects of the styrofoam are shown in Fig. 18. A probe which was placed in a domicile without brood indicated it was warmer on 13 occasions than corresponding external temperatures. During those hours when the air temperature was warmer, the empty domicile was at the most 5.5 C cooler.

Discussion

The three periods of the nest temperature sequence (Hasselrot, 1960) were clearly discernible in the artificial domicile nest. The period of upbuilding was characterized by temperature variations caused by the absence of the foraging queen. Because the volume of the nest had increased during first brood pupal and second brood egg development, the rate of re-warming was slower and total time required by the queen to rewarm the nest was longer than during first brood larval development. The period of equilibrium was characterized by high even nest temperatures which were not in accordance with the outside temperature. As this was the period of maximum nest population, maximum flight activity, and maximum nutritional requirements, the maximum continuous nest temperature was expected. These higher temperatures provide optimum conditions for the work and growth of the colony, and are

accompanying factors for a developmental state necessary for queen production (Cumber, 1949a). The period of decline was characterized by gradually decreasing variations in the nest temperature which came into close agreement with the outside temperature. The decline in the nest temperature is doubtless connected with the lack of honey in the colonies, arising from the sexual forms using up the supply, and from the disintegration of the colony (Hasselrot, 1960).

Results of investigations on the 24-hour temperature in the artificial nest indicated that the maximum and minimum nest temperatures as a rule occurred close to the maximum and minimum diel air temperatures. Worker foraging movement in or out of the nest appeared not to influence the nest temperature. Because of the few lengthy observations, the temperature phenology in the natural nest could not be followed, but I believe that it would be the same as for the artificial nest.

The natural nest temperature was more dependent on the external air temperature and the brood was subjected to more severe environmental factors than the artificial domicile nest which had the protection of the styrofoam lid. Even with these nest temperature differences, the developmental time for each brood did not vary, as did the total nest populations. Generally, more eggs, larvae, pupae, and emerging adults of the second and third brood as well as food availability were found in the artificial domicile nests than in the natural nests.

The bees within the natural nests utilized a thick wax-pollen and moss liverwort canopy which acted as an insulating cover, maintained the nest temperature and protected the brood from the other environmental

factors. The wax-pollen canopy, the moss and liverwort nesting material, the microlocation of the natural nests in a 180-270 degree position at the base of hummocks or moss mounds, and the general location of natural nests in the warmer moss and sedge meadows are adaptations for utilizing solar radiation which allowed the bees to maintain adequately high nest temperatures for brood production.

The danger of overheating the nest through excessive insulation is, according to Himmer (1933), very small. The bees regulated the temperature of the domicile nest by fanning with their wings at the tunnel entrance, thus increasing the air flow. Hasselrot (1960) found that workers began to vibrate their wings at a nest temperature of about 33 C and 13 C in the surrounding air. No workers were observed fanning any of the natural nests as small ventilation holes in the wax-pollen and moss canopies were already present.

The temperature curves obtained for these arctic bumblebees were as high as and similar to the temperature curves obtained by Himmer (1933), Nielsen (1938), Hasselrot (1960), and Wójtowski (1963a, b) for members of other species of bumblebees, and thus were not specially characteristic.

Food Preference

Introduction

The competition between insects for the available nectar and the competition between plants for the services of pollinating insects have been discussed by several authors (Knuth, 1906-1909, Clements and Long, 1923, Grant, 1950, Brian, 1954, Hocking, 1968), and have an important bearing on this study. The purposes of this section were to establish the adaptations and relationships of arctic bumblebees to the arctic flowers. The phenology and constancy of visitation and usage within the nest were also investigated.

Many general, regional studies of pollinators have been made since the publication of Knuth's "Handbook of Flower Pollination" (1906-1909). Some of these are Lovell (1918), Robertson (1895), Løken (1949), Brian (1951b, 1952), Fye and Medler (1954b), Hasselrot (1960), and Macior (1964, 1965, 1966, 1967, 1968a).

The literature on flower constancy for all Apidae was recently reviewed by Grant (1950). Previous investigations are by Christy (1883), Betts (1920, 1935), Clements and Long (1923), Brittain and Newton (1933), Brian (1952, 1954), and Free (1955b). Høeg (1924, 1929) reported on the pollen constancy from Novaya Zemlya and Ellesmere Island, respectively. Cockerell and M'Nary (1902) suggested that arctic bumblebees visit a great variety of plants because they have almost a monopoly, but McAlpine (1965b) and Hocking (1968) disagree.

In the arctic regions pollination biology of plants and pollen on bumblebees has been investigated by McLachlan (1879), Ekstam (1894, 1897, 1899), Jacobsen (1898) in Friese (1902, 1904, 1908, 1923a, b),

Sparre-Schneider (1906), Johansen and Nielsen (1910), Frison (1919), Sladen (1919), Johansen (1921), Høeg (1924, 1929), Richards (1931), Longstaff (1932), Brinck and Wingstrand (1951), Holmen (1957), Bruggeman (1958), Freuchen and Salomonsen (1958), Savile (1959), Gavrilok (1961), Løken (1961), Swales (1966), Milliron and Oliver (1966), Mosquin and Martin (1967), and Hocking (1968).

The pollen of flowering plants plays an important nutritional role in the life of a bumblebee. It is the main source of protein (Auclair and Jamieson, 1958, Weaver and Kuiker, 1951), fat (Hugel, 1962), vitamins (Schwarz and Kock, 1954, Bukatsch and Wildner, 1956) and minerals (Lubliner-Mianowska, 1956) that a bumblebee colony needs to maintain itself.

Sugars (carbohydrates) present in the nectar of flowers of various species have been investigated by Wykes (1952). She found the **mono- and oligosaccharide** (fructose, sucrose, and glucose) occurred in nectar from nearly every species tested and found traces of maltose, melibiose, and raffinose in nectar from flowers of some species. There have been many studies of the factors which influence the amount and concentration of nectar secreted as Park (1930), Hocking (1953, 1968), Wykes (1950, 1951, 1952a, b, c), Manning (1956), and Shuel (1967) have indicated. These studies have shown that the volume and total sugar concentration of nectar secreted by individual flowers varies characteristically in different species, and also within any one species. Thawley (1969) reviewed the composition and properties of honey.

Sladen (1912), Plath (1934), Free and Butler (1959) and Knee and Medler (1965) have described two types of honey found in bumblebee nests

as either "thin" or "thick" honey. Sladen (1912) described thin honey as that found in the honey pots constructed out of wax by the establishing queen and later by workers. He believed this thin honey was freshly gathered and consumed each day. Thick honey was described as being found in old empty cocoons and considered stored for times of scarcity.

The annual duration and seasonal succession of the growth period and the variance between species (Sørensen, 1954, Hocking, 1968), especially during August and September when the abundance of bumblebee flowers was reduced is important to the survival of the bumblebees. Sørensen (1941) in north-east Greenland distinguished five phenological seasons or aspects, which followed each other in rapid succession and which Powell (1961) recognized as being shorter in length at Lake Hazen. Powell (1961) compared the phenology of Lake Hazen, with Alert, N.W.T., and Eskimonae's. Hocking (1968) indicated seasonal peaks for four common species of plants during three different years.

Materials and methods

The behavior of bumblebee foragers on the flowers visited at Lake Hazen was observed. These observations include records of flower species, constancy and possible flower pollinating mechanisms.

To increase the reliability of the visual observations and to indicate which flowers were utilized and for what (pollen and/or nectar), 406 samples of pollen and nectar were taken from 15 nests in 1967 and 134 samples from 22 nests in 1968. The samples consisted of fresh moist pollen from under the larvae and pupae, from the corbiculae of incoming

or field collected foragers, wax from the honey pots, brood and canopy, nectar from the honey pots and brood, and fresh bee faeces. Samples were taken throughout the summer at each brood observation and once from nests destroyed by an arctic fox.

All pollen and nectar from the nest and pollen from corbicular loads were mounted in glycerine jelly tinted with basic fuchsin for identification by comparison with photographs taken from samples in a reference collection prepared from flowers in the research area. Pollen identifications were based on sculpture and form only.

The estimates of total sugars in the honey contained in the honey pots were taken with two pocket refractometers of Bellingham and Stanley design at ranges of 0-50% and 40-85%. These readings were taken with pollen and nectar samples and brood developmental observations.

Flower preferences

In Appendix II, the phenology for 1958 from Powell (1961) and for 1962 in Savile (1964) and from my two summers is presented. A comparison of dates for these four seasons at Lake Hazen shows tremendous variations between seasons, but indicates when the respective "bumblebee flowers" would be visited and utilized for food.

The phenology of bumblebee flowers, the date of first B. polaris (queen, worker, and male) occurrence and the period of utilization for both seasons is presented in Fig. 28. This figure was constructed from the pollen and nectar nest samples and from dates of total visual observations. Total visual observations for the various flower species for which individuals of B. polaris and B. hyperboreus were observed are presented in Table 10.

Table 10

Number of observations of Bombus polaris and B. hyperboreus individuals at flowers of various species at Lake Hazen, N.W.T., 1967 and 1968

	<u>B. (A.) polaris</u>				<u>B. (A.) hyperboreus</u>		
	<u>♀</u>	<u>♂</u>	<u>♀</u>	<u>♂</u>	<u>♀</u>	<u>♂</u>	<u>♀</u>
1967							
Saxifraga oppositifolia	49	1			2		
Salix arctica (♂ ♀)	20	1			1		
Dryas integrifolia	4	44	3		1	1	
Cassiope tetragona		10					
Papaver radicum		2	1				
Pedicularis arctica	30	9			5		
Pedicularis capitata	5	5			4		
Melandrium affine		1					
Stellaria longipes		1	6			1	
Silene acaulis					1		
Arnica alpina		1					
Polygonum viviparum			1				
1968							
Saxifraga oppositifolia	23	3			4		
Salix arctica (♂ ♀)	36	1	2	1	1		
Dryas integrifolia	4	16			5		
Cassiope tetragona		13	3				
Stellaria longipes		10	7				
Pedicularis arctica	23	15			3		

Pedicularis capitata	19	19	2
Saxifraga tricuspidata		8	2
Polygonum viviparum			3
Arnica alpina		1	
Silene acaulis			1
Epilobium latifolium		8	18

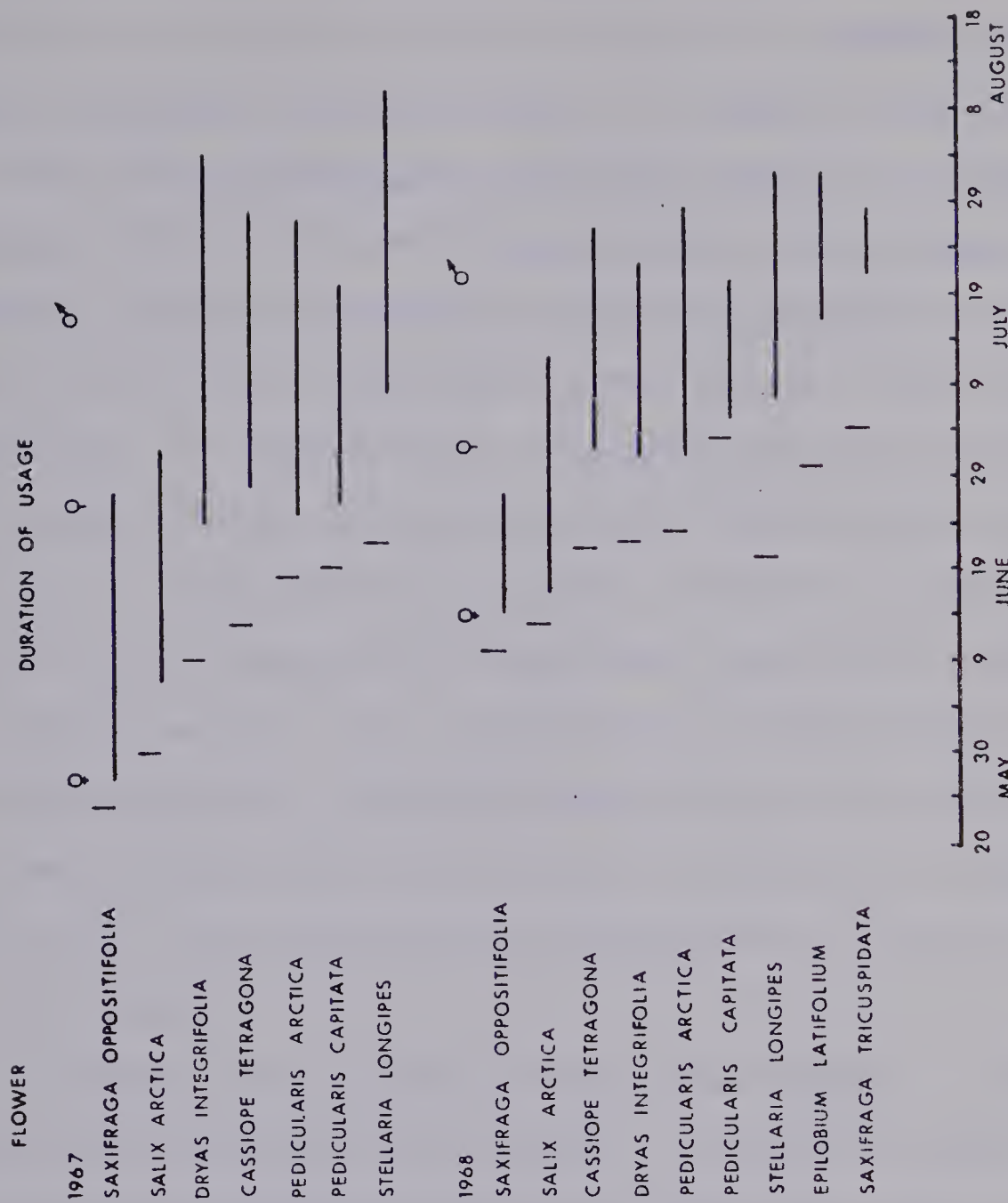


FIG. 28 PERIOD OF UTILIZATION FOR 1967 AND 1968 OF THE MAJOR BUMBLEBEE FLOWERS AT LAKE HAZEN. (Vertical line and symbols indicate first appearance)

The main flowers which bumblebees utilize for feeding larvae and themselves at Lake Hazen are members of the species Saxifraga oppositifolia, Cassiope tetragona, Pedicularis arctica, (P. hirsuta), Salix arctica (male and female), Dryas integrifolia, Pedicularis capitata and Stellaria longipes. Flowers of the species Silene acaulis, Arnica alpina, Polygonum viviparum, Saxifraga tricuspidata and Epilobium latifolium are occasionally visited at the end of a season when the more important flowers are reduced in abundance. A few pollen grains of Cerastium sp. were collected late in the season from three honey pots from two different nests, which indicates that these flowers were sparsely utilized for nectar. The flowers visited at the end of the season were those late in starting and then advanced rapidly. This is indicated in the dates of the flower phenology (Appendix II). Thus the rapidity of the active season affected the flower phenology and flower visitation. As indicated in flight activity data, only nectar was being collected from the flowers at the end of the season.

The composition of 70 pollen pellets was as follows: 35 (50%) consisted of pollen from one plant species, 27 (38.6%) of pollen from two plant species, 6 (8.6%) of pollen from three plant species and 2 (2.8%) of pollen from four plant species. From the 459 visual observations for both summers only 13 consisted of two mixed flower visitations and three consisted of three mixed flower visitations. The rest were single plant visitations. The foragers at Lake Hazen visited a wide range of flowers throughout the season, but at any one time they visited members of a few species only. For example, before workers

emerged, the queens visited only S. oppositifolia and S. arctica flowers, but when these plants were reduced in abundance the foragers visited others.

In this study 254 samples from 12 nests in 1967 were analyzed for concentration. Thin and thick honey was found as Sladen (1912) described. At Lake Hazen honey first appeared when the workers started foraging. Although the number of honey pots increased as the second and third brood larvae were being fed, the number in use declined when the first males emerged. Most of the incoming nectar was placed in the honey pots and it was from these that the sexual adults fed. The concentrations of total sugars were taken from one nest, Fig. 29, from queen acceptance until final brood decay. This indicated a gradual increase in the thin and thick honey concentrations as the brood progressed. Concentrations from other nests indicated this same trend, although some thin honey in some nests was as low as 50.5%. As expected the mean honey concentrations varied from nest to nest and from honey pot to honey pot within the same nest on differing days. Possible reasons for the difference in sugar concentration are water evaporation (Plath, 1934) and quantitative selective feeding (Free, 1955c).

In comparing the total sugar concentrations from the flowers (Hocking, 1953, 1968), with those of the total sugar concentrations of thin and thick honey, the latter is almost always more concentrated, probably because of water evaporation.

The names of the plants which were visited by members of B. polaris and B. hyperboreus are recorded in Appendix III. In total B. polaris and

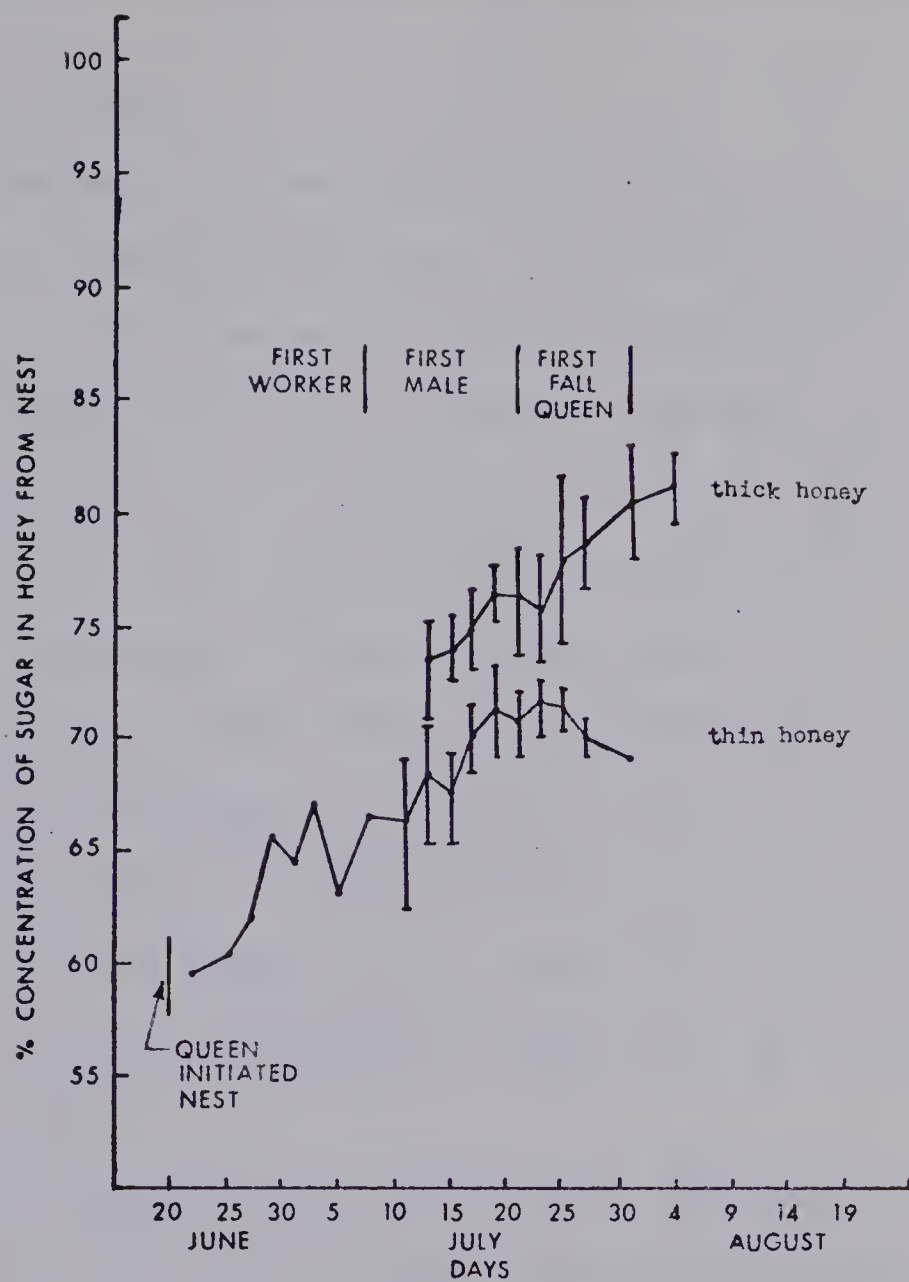


FIG. 29 THE CONCENTRATION OF TOTAL SUGARS FROM THIN AND THICK HONEY FROM ONE NEST THROUGHOUT A SUMMER. (Vertical lines indicate one 3D each side of mean.)

B. hyperboreus have been recorded to visit a total of 18 different families comprised of 36 different genera and 43 different species.

Discussion

The dependence of these bumblebees on flowers for nutrition is perhaps greater than the dependence of the flowers on pollination by the bumblebees. The bees were recorded foraging for pollen and/or nectar from members of 15 plant species at Lake Hazen and from members of 36 different genera in other arctic localities. This alone indicates that 'bees in the arctic tend to become less restricted in their choice of flowers' (Richards, 1931) and that they 'specialize in being unspecialized' (Savile, pers. comm., 1969). The 50% constancy in flower visitation of these arctic bumblebees is in close agreement with the total figure given by Brian (1954) for several authors and various other members of Bombus, but is much higher than the figures given by Høeg (1924, 1929), although he analyzed the pollen from other parts of the body beside the corbiculae.

Almost all plants beyond tree-line are self-fertile, and several are apomictic, necessary safeguards against frequent seasons when insect activity is severely restricted during the period of bloom (Savile, pers. comm., 1969). But, McAlpine (1965a) and Hocking (1968) have stated there are a number of anthophilous Diptera which are important arctic pollinators, a fact which indicates that some cross-pollination occurs in many, perhaps most flower plants. Hocking (1968) believes flowers compete for pollination rather than pollinators competing for nectar. The arctic bumblebees no doubt are pollinators, but only of

those flowers from which they foraged extensively. That other less important bumblebee-visited flowers are doubtful benefactors; however, there are exceptions such as S. longipes and E. latifolium.

As the presence and abundance of the arctic bumblebee visited plant species within the Canadian Arctic Archipelago and generally within the whole arctic varies, the usage by the bumblebees also varies. For example, Silene acaulis which has been recorded by several authors to be extensively abundant and visited by bumblebees on Novaya Zemlya was rare in abundance and visitation at Lake Hazen. Other examples can be found in the Cruciferae, Ericaceae, and especially Leguminosae. The possibility of many ecological niches as yet unoccupied (McAlpine, 1964, 1965a) is another reason for the variable usage by bumblebees. For example, the complete absence of Dryas integrifolia from Ellef Ringes Island (McAlpine, 1965a) seems important, as bumblebees are also not inhabitants, whereas Dryas is an important bumblebee flower at Lake Hazen.

Many of the plants visited by arctic bumblebees have a circumpolar, arctic-alpine distribution, which indicates a sympatric distribution by the bees. However, exceptions occur, such as Papaver radiatum, Saxifraga hirculus and Pedicularis arctica.

The Association between Members of Bombus hyperboreus and Bombus polaris

Introduction

During studies at Lake Hazen it became clear that the behavior of members of B. polaris and B. hyperboreus indicated a host-parasite relationship. Although various species of Bombus show parasitical tendencies (Sladen, 1912, Lindhard, 1912, Plath, 1934, Hobbs, 1965b, 1967b), the **host-parasite** relationship discussed here is unique because, unlike other Bombus queens, the B. hyperboreus queens do not establish nests of their own in most of their distribution. Thus the parasitic behavior of individuals of B. hyperboreus is analogous to the parasitic behavior of Psithyrus individuals, the true parasite of Bombus. The origin of Psithyrus has given rise to much speculation. Most authors agree that the genus Psithyrus shares a common ancestry with Bombus. The morphological evidence associated with the loss of certain food gathering structures indicates a monophyletic origin (Gascholt, 1922, Richards, 1927) whereas behaviorally a polyphyletic origin seems the more probable (Richards, 1927). By studying individuals of B. hyperboreus some important aspects as to the evolution of the parasitic Psithyrus group may be demonstrated.

Previous publications on Psithyrus by Sladen (1899, 1912), Wheeler (1919), Gaschott (1922), Plath (1922b, 1934), Frison (1926), Richards (1927), Reinig (1935), Cumber (1949b), Free and Butler (1959), Hasselrot (1960), Hobbs, Virostek and Nummi (1960), Webb (1961), Hobbs, Nummi, and Virostek (1962) and Hobbs (1965a, b, 1966a, b, 1967a, b, 1968) have been consulted. A solitary form of life with few or no workers produced was indicated for B. hyperboreus, B. balteatus, and B. polaris by Friese

(1902, 1904, 1908, 1923a, b) and Friese and Wagner (1912). They did not suggest a parasite-host relationship among members of these species. However, Milliron and Oliver (1966) made preliminary observations on a usurpation at Lake Hazen by B. hyperboreus individuals of nests of B. polaris.

As Wheeler (1919) points out a special type of parasitism amongst aculeate Hymenoptera occurs, for the host and parasite are always related to one another, often very closely. Bombus and Psithyrus are closely related genera, hardly distinguishable except by the loss of the pollen-collecting apparatus in the latter. Although the B. hyperboreus queens have pollen-collecting corbiculae they were never observed to collect pollen, except on the ventral body hairs from such a flower as Salix arctica. As in Psithyrus specimens the tongues of B. hyperboreus specimens have not been affected, since the bees visit a wide variety of flowers. Perhaps of some significance is that the malar space of a female Psithyrus is always shorter, at least slightly, than most of its hosts (Richards, 1927), whereas individuals of B. hyperboreus have the largest malar space of any Alpinobombus and were known by many early authors for their large robust size. Individuals of B. hyperboreus as typical members of Bombus do not possess any of the morphological characteristics of Psithyrus which Richards (1927) used for comparison between these two genera. Reinig (1935) compiled a list of Psithyrus species together with their Bombus hosts, and came to the conclusion that the Psithyrus in most cases strongly resembles her principle host. The color resemblance between these two Bombus species (polaris and hyperboreus) has led to lengthy synonymies. Their geographical variation in the color patterns

may be similar. Since both are living under the same ecological, geographical and climatic conditions, the genetic constitution they have in common is likely to have been influenced in the same direction, and hence they often have attained similar coloration.

Observations

The ranges of B. hyperboreus and B. polaris are similar. Individuals of B. hyperboreus emerged later in the season and were not as abundant as those of B. polaris. The nest-seeking behavior was similar to B. polaris, although individuals of B. hyperboreus were not observed to initiate nests of their own. The absence of workers of B. hyperboreus is significant, but Jacobson (1898) in Friese (1902, 1904, 1908, 1923a) reported collection of a few workers on Novaya Zemlya and Friese and Wagner (1912) reported a few workers from Norway and Sweden. Richards (1931) reported observing a worker to female ratio of 0.2, and Milliron and Oliver (1966) reported examining about a dozen museum specimens of B. hyperboreus workers mostly from Scandinavia. Most authors (Strand, 1905, Richards, 1931, Henriksen, 1937, 1939, Brinck and Wingstrand, 1951, Bruggeman, 1958, Milliron and Oliver, 1966 and myself) collected only B. hyperboreus queens and males from various localities.

Queen B. hyperboreus searched primarily along cracks in the clay and in lemming holes for nesting sites of B. polaris. They usually flew less than 25 cm above the ground, hovering slightly at the entrance before continued flying or alighted to investigate more thoroughly. Most B. hyperboreus queens were seen just previous to or after the first worker emergence although several were still nest-searching days after

the first worker emerged. Perhaps a B. hyperboreus queen has a continuing threshold for searching until it locates a B. polaris nest.

The following is a description of a B. hyperboreus queen from the time of her first discovery of a B. polaris natural nest until she remained within the nest 58 minutes. The observation was made June 28, 1967, from 0030 to 0330 on a clear, calm, 9.0 C night in a marsh sedge meadow (M8).

The B. hyperboreus queen first approached the nest flying at a height of less than 25 cm. She flew three to four orientation circles before landing and entering the 210° facing entrance. After defensive behavior (i.e., rapid movement of the wings) from workers she retreated from the nest to a nearby moss clump where she groomed herself. Grooming consisted of rubbing the fore- and mid-legs over the head and thorax and hind-legs over the sides of the abdomen or together. She was repelled from the nest 13 times by the workers and queen before she gained acceptance. Twice the workers blocked the entrance of the intruding queen by lying upside down with the stinger protruding and once two workers followed her about 60-75 cm from the nest. The B. hyperboreus queen after being repelled from the nest either visited flowers (of the species Dryas integrifolia, Salix arctica, Saxifraga oppositifolia, Pedicularis arctica) for nectar or groomed. The grooming procedure was repeated many times. The B. hyperboreus queen did not orient back to the nest in the latter part of the behavior, but flew directly .

Examining the nest at 0830 the same morning I found the B. polaris queen dead beside the honey pot and near the nest entrance, eight B.

polaris workers (some were collecting pollen and nectar and others were warming the brood), eight first brood pupae near emergence, and an active B. hyperboreus queen. During the examination the queen remained (except when I moved her) on top of a rough new egg cell built on the side of the incubation groove at 6 to 9 o'clock position. This egg cell contained seven horizontally laid eggs. As the queen appeared to be protecting this egg cell, I presumed she had laid the eggs. Other contents of the nest included 13 early second brood larvae which was the same as the nest contained on the previous day's observation. An arctic fox destroyed this nest two days later; thus observations were terminated.

In five nests which had living B. hyperboreus queens, the host B. polaris queen was dead. In comparison, Psithyrus queens either kill the host queen, or the workers kill their own queen, or the host queen leaves the nest, or the host queen, workers and Psithyrus live in association within the same nest with the Psithyrus being at first passive and finally dominant. More than one B. hyperboreus queen was collected in one nest with the latest nest-seeking queen alive. Seventeen dead B. hyperboreus queens were found in B. polaris nests as victims of an arctic fox. Milliron and Oliver (1966) reported two composite nests of B. polaris and B. hyperboreus sexuals, as adults or brood. They hypothesized the establishing B. polaris queen was driven off by the usurping B. hyperboreus queen.

In 13 natural nests a conspecific B. polaris queen was found after the original queen had initiated and established a first brood. In all cases one of the two queens was dead and lodged in the moss nesting covering and of five instances known the foundress was the victor of a

previous fight, three instances when the intruder was victor, and five unknown. The intruding conspecific queens were observed nest-seeking late in the season, at least as late as first brood early emergence. The intruding queens did not initiate brood of their own but assisted the foraging workers. No disturbances such as the removal of larvae or the destruction of egg cells were noted in the nests. Milliron and Oliver (1966) reported a single invasion by conspecific B. polaris queens.

Discussion

The immediate cause of parasitism as Wheeler (1919) suggested, may be urgency of oviposition, combined with local or temporary lack of nest-building material, of nest-site or of larval food. Perhaps the parasitic behavior of the B. hyperboreus queens resulted from late emergence in the season, from unfavourable hibernating sites, from infertility, or from a high physiological threshold for initiating their own nests. The availability of adequate nesting sites would not be a factor.

Sladen (1912) observed similar behavior for other species and suggested how aculeate parasitism may have arisen. Richards (1927) wrote that a bumblebee queen nearly always 'parasitizes' colonies of her own or of a closely related species, and this habit would lead to a polyphyletic origin of bees of the genus Psithyrus, "each species being restricted to one or to a few related species." He suggested a preference for a not too unfamiliar nest-odour. Hobbs (1965b, 1967b) observed intra- and inter-specific supersedures, but he had not observed any inter-subgeneric supersedures.

Latter (1906), Sladen (1912), Plath (1934), Free and Butler (1959) and Hobbs (1967a) believe that the scent of the host colony allows the associate to find the nest. Similarly I believe the scent of the host colony allowed the queen B. hyperboreus to locate the nest, although, later in acceptance behavior, sight (through orientation) was predominant. Of significance was the behavior which the queen established herself in the nest. Presumably odours of members of closely related species are similar, yet the queen camouflaged her own body smell and acquired that of the nest or possibly that of the flowers (by pollen) she visited. The repeated rubbing and grooming of her body and legs was interpreted as part of this disguise.

Richards (1927) suggested that parasitic aculeate as a whole tend to resemble southern races of industrious species in their color and pubescence. This may indicate that species tend to become parasitic at the northern edge of their range, the adverse conditions there encountered tending to make permanent the temporary and local parasitism which is not uncommon within many species. Reinig (1935) studied the geographical distribution of individual bumblebee species and their particular parasitic Psithyrus species. He found that their distribution may coincide completely, generally the range of the parasite not exceeding the limits of the host species range. In this case the distribution of B. hyperboreus and B. polaris individuals are similar and thus substantiates Reinig (1935).

Although morphological evidence associated with the loss of food gathering structures indicates a monophyletic origin, the species of Psithyrus are more distinct from one another than are the members of

any subgenus of Bombus. Thus although the parasites do not structurally resemble their hosts, there is at least some evidence that the genus Psithyrus is polyphyletic (Richards, 1927). Based on behavioral evidence, I believe that the polyphyletic origin of Psithyrus is more probable, each subgenus of Psithyrus probably arising from a specific Bombus subgenus. Once the Psithyrus parasite has sufficiently evolved on its Bombus host then they parasitize other subgenera of Bombus. Reinig (1935) stated that Psithyrus species are scarce at high altitudes and latitudes (the distribution of members of Alpinobombus) and that as far as I know, no Psithyrus parasitises any members of Alpinobombus. Thus I believe on behavioral evidence that the origin of parasitism within the Alpinobombus group is still developing in the B. hyperboreus-polaris relationship and that with time B. hyperboreus will come to morphologically resemble members of Psithyrus.

General Discussion and Conclusions

With the previous discussion of specific differences in behavior and ecology as a background, it may be profitable to ask how members of Alpinobombus came to have the particular set of behavior patterns they now possess. In other words, what has been the evolution of behavior in the subgenus? It may be desirable to list some of the behavioral characteristics considered primitive and those considered specialized. The survival value of the various modifications of behavior may then be considered.

The criteria for deciding which attributes should be considered primitive and which advanced have been discussed by Evans (1957, 1966). He considers: 1. In an array of specific differences having to do with a given unit of behavior, those characteristics are primitive which most closely resemble those of the less modified members of related genera. 2. If a behavior pattern which occurs in one or a few members of a genus also appears in the primitive members of closely related genera, then that behavior pattern is primitive. 3. If a behavior pattern is unique or occurs only sporadically in the derived forms of related genera, then that behavior pattern is specialized.

As the arctic climatic environmental factors (i.e., low temperature, small heat budget, and reduced growing season) are more severe than the other world regions, the Alpinobombus bees have developed unique or specialized behavior responses to these environmental factors. Important among these behavioral responses is the habitat in which the queen establishes her nest. Most species of bumblebees often make their nests in the abandoned nests of field-mice, voles, shrews, and birds,

either on or below the ground surface--nests which consist of accumulations of fine pieces of grass, moss, leaves, and other material collected by the former occupant. Generally the queens of most species of Bombus are fairly versatile in their choice of habitat, however some species seem to have preferences for definite types of localities. The arctic bumblebees are among those who choose a preferred habitat; a habitat such as the marsh and sedge meadow which is warmer and drier than most areas the queens nest search. Also these meadows have more suitable nesting material than other less vegetated areas (i.e., sand, clay, gravel knolls, or Dryas-Kobresia hummocks) and the queen can construct a nest for herself on the surface of the ground instead of using the deserted nest of a small mammal. The arctic queens utilize the incoming solar radiation by choosing the warmest sector of Dryas hummocks or moss mounds in which to establish her nest.

Unfortunately the brood-rearing behavior of most of the 35 subgenera (Richards, 1968) of bumblebees is unknown; however Hobbs (1964a) studied the phylogeny of seven of nine subgenera of North American bumblebees. The evolutionary position of members of Alpinobombus based on primitive and specialized brood-rearing characteristics was included in his phylogeny and thus pertinent aspects of that study are included here. He hypothesized that if the feeding of pollen and honey separately and the feeding of larvae collectively are considered primitive, members of species of Subterraneobombus would be considered the most primitive. Members of species of Alpinobombus and Fervidobombus would be considered more advanced because they feed male and queen broods with mixtures of pollen and honey. Members of species of Pyrobombus represent the link between

the primitive and more advanced forms in that they prime with pollen some of the egg cells of the second and succeeding broods. Members of species of Bombus and Cullumanobombus rear early-instar larvae of the second and succeeding broods collectively in unprimed cells. The species of Bombias could be considered the most advanced because their members feed all larvae individually and rear all but the first broods in unprimed cells, and therefore more closely resemble species of the genus Apis L. The position of these seven subgenera may change as more characteristics through further studies are completed.

Also of evolutionary significance to the survival of arctic bumblebees is that queens of Alpinobombus species are the only ones known to place all eggs in single egg cells in the first brood. Queens of other subgenera of Bombus construct adjoining cells of pollen and lay a single egg in each. The time required by the arctic queen to construct egg cells, incubate the eggs, larvae, and pupae, and collectively feed the larvae is minimal and if correlated with the reduced growing season is more efficient than other subgenera of Bombus. The production of a higher number of workers in the first brood of members of Alpinobombus in comparison to members of other subgenera may perhaps be related to the following production of the second (male) and third (female) broods. The large number of workers in the first brood and the production of the sexual brood are also related to the reduced growing season.

A unique meteorological condition in the arctic is that the daily range of light intensity is small; and that insects are unable to use the 24 hour rhythm either to control activity directly or for the uniform setting of an endogenous cycle (Corbet in Downes, 1965). In

temperate regions the daily range of light intensity is large, thus insects are able to establish endogenous cycles. Perhaps generally bumblebee flight in these regions is related to the light intensity and temperature fluctuations. However, in the arctic, shifts in bumblebee flight activity occurred and are considered fortuitous responses to the continuous 24 hours of light. The queens ceased flying 24 hours when the workers commenced foraging, only to resume again near the end of the season. The workers, which it is believed, tended to take their cues for a 24 hour rhythm from the height and position of the sun, gradually increased the length of forage until at the seasons end they were flying 24 hours.

There are structural and functional adaptations for flight at low temperatures. The large hairy appearance and dark coloration are factors which allow the bumblebees to be warmed by solar radiation, and the relatively low flying height suggests the bees attain body warmth from the reflected radiation of the soil. These factors are considered specialized in members of Alpinobombus and some members of Pyrobombus which inhabit a Boreal-Cordilleran transition zone in the mountains. In comparison other members of Pyrobombus and members of other subgenera have shorter uniform hair and inhabit lower altitudes and latitudes.

To indicate if flower visitation in the arctic is primitive or specialized is useless as all bumblebees utilize flowers for nutrition. Even the pollinating mechanisms on the flowers differ. The visitation of an unusually wide range of flowers for nutrition may be interpreted as exclusiveness in being unexclusive. Because the presence and abundance of the various bumblebee flowers within the arctic varies, the

usage by the bumblebees also varies. This usage varied with the relative lengths of time the flowers were in bloom.

According to present theory, competition, by favouring increased specialization in the use of the total resources, allows the establishment of new species. But, perhaps in the arctic at present selection and adaptation are less intense or precise, because of the lack in diversity of species. Despite these low numbers of species and many unoccupied ecological niches (McAlpine, 1964, 1965a), associations have developed (i.e., B. polaris-hyperboreus host-parasite relationship) and these may be followed by modifications of the dynamics of the populations even though the evolutionary process is probably slower in the arctic and is always liable to be set back by climatic disasters (Downes, 1962, 1964). Competition in this case which is analagous to the behavior of members of Psithyrus may have developed from the later emergence of the B. hyperboreus queens, from urgency of oviposition, or from a low physiological threshold for initiating their own nests.

The bumblebees composing part of the arctic ecosystem tend to be variable in their form, responses, and tolerances, and are continually adapting their habits to the existing climatic environmental factors. Temperature is generally considered to be first importance here, followed by sky illumination or those associated directly with solar radiation. Even these responses and tolerances may vary within themselves in relation to the different parts of the distribution range. As more species are able to overcome some of the limiting physiological factors, and as the numbers of members of a species increases, their

adaptations will tend to become more complex and the rate of evolution will increase. And thus the polar regions although appearing to be in temporary equilibrium on the shorter time-scale, are in a constant development in complexity.

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Appendix I

Mosses and liverworts associated with bumblebee natural nests collected in 1967 and 1968 from Hazen

Camp area, Ellesmere Island, N.W.Y.

abundance within samples are 4=dominant, 3=abundant, 2=small or medium quantity, 1=trace, 0=none

<u>bryophytes from nests</u>	<u>abundance</u>											
	<u>1967</u>					<u>1968</u>						
	no. of <u>nests found</u>	0	1	2	3	4	no. of <u>nests found</u>					
<u>Fissidens arcticus</u> Bryhn	1	46	1	0	0	0	0	46	0	0	0	0
<u>Distichium</u> sp.	10	36	8	2	0	0	5	41	5	0	0	0
<u>Distichium capillaceum</u> Hedw.) BSG.	21	25	15	6	0	0	19	27	17	2	0	0
<u>Distichium hagenii</u> Ryan ex Philib.	1	46	1	0	0	0	0	0	0	0	0	0
<u>Ditrichium flexicaule</u> (Schwaeger.)	19	29	12	5	0	0	19	27	10	6	3	0
<u>Oncophorus wahlenbergii</u> Brid.	1	46	1	0	0	0	1	46	1	0	0	0
<u>Bryobrittonia pellucida</u> Williams	1	46	1	0	0	0	1	45	1	0	0	0
<u>Encalypta alpina</u> Sm.	3	43	3	0	0	0	2	44	2	0	0	0
<u>Encalypta procera</u> Bruch	2	44	2	0	0	0	3	43	3	0	0	0
<u>Barbula icmadophila</u> Schimp. ex Mull	10	47	9	1	0	0	5	41	5	0	0	0
<u>Bryoerythrophyllum recurvirostrum</u> (hedw.) Chen	6	41	5	1	0	0	7	39	6	1	0	0
												150

<u>Gymnostomum recurvirostrum</u> Hedw.	2	45	2	0	0	0	1	45	1	0	0	0
<u>Pottia heimii</u> (Hedw.) Hampe	1	46	1	0	0	0	0	46	0	0	0	0
<u>Tortella fragilis</u> (drumm.) Limpr.	1	46	1	0	0	0	0	0	0	0	0	0
<u>Tortella arctica</u> (Arnell) Grundw & Nyh.	0	0	0	0	0	0	1	45	1	0	0	0
<u>Tortula ruralis</u> (Hedw.) Gaertn., Meyer & Scherb	1	46	1	0	0	0	0	0	0	0	0	0
<u>Tortula norvegica</u> (Web.) Wahlenb <u>ex</u> Lindb.		0	0	0	0	0	1	45	1	0	0	0
<u>Bryum neodamense</u> Itzigs	2	45	2	0	0	0	2	44	2	0	0	0
<u>Bryum angustirete</u> Kindb. <u>ex</u> Mac.	2	45	1	1	0	0	0	0	0	0	0	0
<u>Bryum</u> sp.	38	9	31	7	0	0	33	13	33	0	0	0
<u>Pohlia</u> sp.	1	46	1	0	0	0	0	0	0	0	0	0
<u>Cinclidium arcticum</u> Schimp.	6	41	5	1	0	0	2	34	9	2	1	0
<u>Cyrtomium hymenophyllum</u> (BSG.) Holmen	2	45	2	0	0	0	6	40	4	1	1	0
<u>Mnium blyttii</u> BSG.	1	46	0	0	1	0	1	45	1	0	0	0
<u>Meesia trifaria</u> Crum, Steere & Anderson	2	45	1	1	0	0	2	44	0	0	2	0
<u>Mnium orthorhynchum</u> Brid.	0	0	0	0	0	0	1	45	1	0	0	0
<u>Mnium</u> sp.	0	0	0	0	0	0	1	45	1	0	0	0
<u>Aulacomnium palustre</u> (Hedw.) Schwaegr	0	0	0	0	0	0	1	45	0	1	0	0
<u>Aulacomnium turgidum</u> Wahlenb.) Schwaegr	0	0	0	0	0	0	1	45	0	1	0	0

<u>Messia uliginosa</u> Hedw.	0	0	0	0	0	0	0	4	42	4	0	0	0
<u>Catoscopium nigritum</u> (Hedw.) Brid.	1	46	1	0	0	0	0	2	44	2	0	0	0
<u>Philonotis fontana</u> (Hedw.) Brid.	7	40	6	0	1	0	0	6	39	6	1	0	0
<u>Timmia austriaca</u> Hedw	2	45	1	1	0	0	0	2	44	2	0	0	0
<u>Myurella julacea</u> (Schwaegr.) BSG.	2	45	2	0	0	0	0	0	0	0	0	0	0
<u>Timmia norvegica</u> Zett.	0	0	0	0	0	0	0	2	44	2	0	0	0
<u>Myruella tenerima</u> (Brid.) Lindb.	2	45	2	0	0	0	0	0	0	0	0	0	0
<u>Calliargon giganteum</u> (Schimp.) Kindb.	11	36	6	2	1	0	0	14	32	3	7	3	1
<u>Campylium arcticum</u> (Williams) Broth.	36	11	15	13	4	4	4	25	21	6	14	4	1
<u>Cratoneuron arcticum</u> Steere	3	44	1	1	1	0	0	0	0	0	0	0	0
<u>Cratoneuron filicinum</u> (Hedw.) Spruce	7	40	4	2	1	0	0	4	42	0	4	0	0
<u>Drepanocladus aduncus</u> (Hedw.) Warnst.	14	33	1	3	3	5	8	8	38	0	6	1	1
<u>Drepanocladus badius</u> (Hartm.) Roth	1	46	1	0	0	0	0	0	0	0	0	0	0
<u>Drepanocladus brevifolius</u> (Lindb.) Warnst.	5	42	0	2	1	1	6	6	40	1	2	2	1
<u>Drepanocladus revolvens</u> (SW) Warnst	20	26	2	9	3	6	28	28	18	2	15	7	2
<u>Drepanocladus uncinatus</u> (Hedw.) Warnst	0	0	0	0	0	0	0	1	45	0	0	0	1
<u>Drepanocladus vernicosus</u> (Hartm.) Warnst	0	0	0	0	0	0	0	1	45	0	0	1	0
<u>Scorpidium turgescens</u> (T. Jens.) Loeske	4	43	4	0	0	0	0	1	45	1	0	0	0

<u>Lophozia</u> sp.	7	40	6	1	0	0	2	44	2	0	0	0
<u>Riccardia pinguis</u> (L.) Gray	0	0	0	0	0	0	2	44	2	0	0	0
<u>Scapania gymnostomophila</u> Kaalaas	0	0	0	0	0	0	1	45	1	0	0	0
<u>Scapania</u> sp.	0	0	0	0	0	0	1	45	1	0	0	0
<u>Tritomaria quinquedentata</u> (Huds.) Buch	0	0	0	0	0	0	1	45	1	0	0	0
<u>Solenostoma</u> sp.	1	46	1	0	0	0	0	0	0	0	0	0

Appendix II

Phenology of Flowers at Lake Hazen, N.W.T.

Date	1958	1962	1967	1968
	(Powell 1961)	Savile 1964)		
May 24				<u>Saxifraga oppositifolia</u>
30				<u>Salix arctica</u> (male)
June 1				<u>Draba</u> spp.
2				<u>Salix arctica</u> (female)
4	<u>Saxifraga oppositifolia</u>			
	<u>Salix arctica</u>			
7		<u>Saxifraga oppositifolia</u>		
		<u>Lesquerella arctica</u>		
9			<u>Dryas integrifolia</u>	
			<u>Oxyria digyna</u>	
10			<u>Lesquerella arctica</u>	<u>Saxifraga oppositifolia</u>
			<u>Eryaimum pallasii</u>	
			<u>Eriophorum triste</u>	
12	<u>Lesquerella arctica</u>			
	<u>Melandrium triflorum</u>			
	<u>Potentilla nivea</u>			

June 13

Salix arctica (male)

Cassiope tetragona

Lesquerella arctica-

Salix arctica (female)

Draba spp.

14 Cassiope tetragona

Braya humilis

Oxytia digyna

Carex rupestris

Carex nardina

15 Stellaria longipes

Dryas integrifolia

Salix arctica (male)

Ranunculus sulphureus

16 Cerastium alpinum

Erigeron compositus

Draba belli

Braya purpurascens

Dryas integrifolia

Erigeron compositus

17

Oxyria digyna

Oxyria digyna

Erysimum pallasii

Potentilla chamissonis

Eriophorum triste

Pedicularis arctica

18

June 18	<u>Cassiope tetragona</u>	<u>Erigeron compositus</u>
	<u>Stellaria edwardsii</u>	
19	<u>Taraxacum arctogenum</u>	<u>Pedicularis capitata</u>
		<u>Taraxacum arctogenum</u>
		<u>Potentilla chamissonis</u>
20	<u>Taraxacum pumilum</u>	<u>Stellaria longipes</u>
	<u>Pedicularis arctica</u>	<u>Eriophorum triste</u>
	<u>Epilobium latifolium</u>	<u>Erysimum pallasii</u>
	<u>Papaver radiculatum</u>	
	<u>Carex rupestris</u>	
	<u>Arenaria rubella</u>	
	<u>Cerastium alpinum</u>	
21		<u>Arenaria rubella</u>
		<u>Cassiope tetragona</u>
22	<u>Arenaria rubella</u>	<u>Dryas integrifolia</u>
	<u>Papaver radiculatum</u>	<u>Potentilla chamissonis</u>
		<u>Eriophorum scheuchzeri</u>
23		<u>Erigeron compositus</u>
		<u>Melandrium triflorum</u>

June 24	<u>Pedicularis capitata</u>	<u>Melandrium triflorum</u>	<u>Pedicularis arctica</u>
25			<u>Papaver radicatum</u>
26			<u>Taraxacum arctogenum</u>
			<u>Pedicularis hirsuta</u>
27		<u>Saxifraga tricuspidata</u>	<u>Cerastium alpinum</u>
28	<u>Eriophorum scheuchzeri</u>		<u>Pedicularis sudetica</u>
	<u>Draba cinerea</u>		
	<u>Pedicularis hirsuta</u>		
29		<u>Cerastium alpinum</u>	
30		<u>Melandrium apetala</u>	<u>Epilobium latifolium</u>
July 1	<u>Silene acaulis</u>	<u>Ranunculus trichophyllus</u>	
	<u>Cardamine bellidifolia</u>		
	<u>Draba lactea</u>		
	<u>Saxifraga caespitosa</u>		
	<u>Saxifraga flagellaris</u>		
	<u>Saxifraga tricuspidata</u>		
	<u>Epilobium latifolium</u>		

July	2	<u>Poa abbreviata</u>			
	3	<u>Eutrema edwardsii</u>		<u>Polygonum viviparum</u>	<u>Pedicularis capitata</u>
	4	<u>Saxifraga nivalis</u>	<u>Saxifraga hirculus</u>	<u>Polygonum viviparum</u>	<u>Saxifraga tricuspidata</u>
					<u>Melandrium triflorum</u>
					<u>Arnica alpina</u>
	5	<u>Trisetum spicatum</u>			
		<u>Luzula confusa</u>			
		<u>Saxifraga cernua</u>			
		<u>Saxifraga rivularis</u>			
		<u>Taraxacum phymatocarpum</u>			
	6	<u>Polygonum viviparum</u>	<u>Trisetum spicatum</u>		
		<u>Melandrium apetalum</u>			
		<u>Saxifraga tenuis</u>			
		<u>Arnica alpina</u>			
	10		<u>Poa hartzii</u>		
	11			<u>Salix arctica</u> (capsule dehisce)	
	12	<u>Phippsia algida</u>			

Appendix III

Literature records of species visited by B. polaris and B. hyperboreus.

References are listed by number: 1. McLachlan (1879), 2. Ekstam (1894), 3. Ekstam (1897), 4. Ekstam (1899), 5. Friese (1902), 6. Friese (1904), 7. Knuth (1906-1909), 8. Sparee-Schneider (1906), 9. Friese (1908), 10. Johansen and Nielsen (1910), 11. Frison (1919), 12. Sladen (1919), 13. Johansen (1921), 14. Friese (1923a), 15. Friese (1923b), 16. Høeg (1924), 17. Høeg (1929), 18. Richards (1931), 19. Longstaff (1932), 20. Brinck and Wingstrand (1951), 21. Holmen (1957), 22. Bruggeman (1958), 23. Freuchen and Salomonsen (1958), 24. Savile (1959), 25. Gavrilick (1961), 26. Løken (1961), 27. Savile (1964), 28. Swales (1966), 29. Milliron and Oliver (1966), 30. Mosquin and Martin (1967), 31. Hocking (1968).

Flower	bee species	reference
Iridaceae		
<u>Iris</u>	<u>polaris</u>	13
Salicaceae		
<u>Salix</u> sp.	both	11, 17, 19
	<u>polaris</u>	26
	<u>hyperboreus</u>	20
	---	10, 23
<u>Salix arctica</u> Pall.	<u>polaris</u>	29, 31
	---	21
<u>Salix nigricans</u>	---	7
<u>Salix glauca</u> L.	---	7

<u>Salix lapponicus</u>	---	7
<u>Salix phylicifolia</u>	---	7
Caryophyllaceae		
<u>Cerastium</u> sp.	<u>polaris</u>	16
<u>Melandrium apetalum</u> (L.) Fenzl.	---	24
<u>Silene acaulis</u> (L.)	both	16
	<u>polaris</u>	29, 31
	<u>hyperboreus</u>	8, 17
	---	3
<u>Stellaris longipes</u> Goldie	<u>polaris</u>	31
Ranunculaceae		
<u>Aconitum</u> sp.	<u>polaris</u>	13
<u>Delphinium</u> sp.	<u>polaris</u>	13
Papaveraceae		
<u>Papaver radicatum</u> Rottb.	<u>polaris</u>	29, 31
Cruciferae		
<u>Hesperis</u>	---	11
<u>Braya purpurascens</u> (R.Br.) Bunge	<u>polaris</u>	16
<u>Parrya nuclicaulis</u> (L.) Regel	<u>hyperboreus</u>	25
	---	2, 3
Saxifragaceae		
<u>Saxifraga</u> sp.	<u>polaris</u>	10, 17
	---	11, 23
<u>Saxifraga oppositifolia</u> L.	both	16
	<u>polaris</u>	29, 31
	<u>hyperboreus</u>	17
	---	2, 3, 24

<u>Saxifraga aizoides</u> L.	both	16
<u>Saxifraga hirculus</u> L.	<u>polaris</u>	16
Rosaceae		
<u>Dryas</u> sp.	<u>polaris</u>	16, 17
	<u>hyperboreus</u>	8, 20, 25
	---	11
<u>Dryas integrifolia</u> M. Vahl.	<u>polaris</u>	29, 31
	---	24
<u>Potentilla</u> sp.	<u>polaris</u>	10
	---	11, 23
<u>Potentilla erecta</u> (L.) Rausch	<u>polaris</u>	26
Leguminosae		
<u>Astragalus</u> sp.	<u>polaris</u>	16
	<u>hyperboreus</u>	20
<u>Astragalus alpinus</u> L.	<u>polaris</u>	22, 28, 30
	<u>hyperboreus</u>	8
	---	3, 5
<u>Oxytropis</u> sp.	both	16
<u>Oxytropis campestris</u> (Rydb.) Barn.	<u>hyperboreus</u>	5, 6, 9, 14, 15
	---	3
<u>Oxytropis maydelliana</u> Trautv.	<u>hyperboreus</u>	25
<u>Oxytropis borealis</u> DC.	<u>hyperboreus</u>	25
Onagraceae		
<u>Epilobium latifolium</u> L.	both	31
	<u>polaris</u>	29
	---	13

<u>Epilobium</u> <u>spicatum</u> Britton	<u>polaris</u>	13
<u>Chamaenerium</u> <u>angustifolium</u> (L.) Scop.	both	19
Ericaceae		
<u>Ledum</u> <u>groenlandicum</u> (Oeder) Hult.	both	18
<u>Cassiope</u> sp.	<u>polaris</u>	10
	---	11
<u>Cassiope</u> <u>tetragona</u> (L.) D. Don.	<u>polaris</u>	17, 28, 31
<u>Phyllodoce</u> <u>coreulea</u> (L.) Bab.	<u>hyperboreus</u>	25
<u>Rhododendron</u> sp.	---	11
<u>Vaccinium</u> sp.	<u>polaris</u>	25
	<u>hyperboreus</u>	26
<u>Vaccinium</u> <u>uliginosum</u> L.	<u>polaris</u>	5
	<u>hyperboreus</u>	18
	---	24
<u>Vaccinium</u> <u>oxycoccus</u>	<u>polaris</u>	5
<u>Vaccinium</u> <u>myrtillus</u>	<u>polaris</u>	5
<u>Arctous</u> sp.	<u>hyperboreus</u>	25
<u>Loiseleuria</u> sp.	<u>hyperboreus</u>	25
Polemoniaceae		
<u>Polemonium</u> <u>boreale</u> Adam	<u>polaris</u>	16
Boraginaceae		
<u>Eritrichium</u> sp.	<u>hyperboreus</u>	25
Scrophulariaceae		
<u>Lagotis</u> sp.	<u>hyperboreus</u>	25
<u>Pedicularis</u> sp.	<u>polaris</u>	10, 27, 29
	---	1, 2, 11, 23

<u>Pedicularis arctica</u> R. Br. + <u>P. hirsuta</u> L.	<u>polaris</u>	31
	---	24
<u>Pedicularis capitata</u> Adams	<u>polaris</u>	31
<u>Pedicularis sudetica</u> Willd.	<u>hyperboreus</u>	3
<u>Pedicularis lapponica</u> L.	<u>hyperboreus</u>	8, 20
<u>Pedicularis lanata</u> Cham. and Schlecht	<u>polaris</u>	13
<u>Bartsia alpina</u> L.	<u>polaris</u>	18, 26

Valerianaceae

<u>Valeriana capitata</u> Pall.	<u>polaris</u>	16
	---	3

Campanulaceae

<u>Campanula</u> sp.	<u>polaris</u>	13, 26
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Compositae

<u>Petasites frigidus</u> (L.) Friese	<u>polaris</u>	30
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